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RESTORING FOREST HABITAT ON ABANDONED FIELDS USING HYBRID POPLAR PLANTATIONS: UNDERSTORY ATTRIBUTES AND SUITABILITY FOR FOREST UNDERSTORY PLANTS

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LA RESTAURATION D'HABITAT FORESTIER EN FRICHES AGRICOLES PAR LES PLANTATIONS DE PEUPLIER HYBRIDE : ATTRIBUTS DE SOUS-BOIS ET VALEUR POUR LES PLANTES FORESTIÈRES DE SOUS-BOIS

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RÉSUMÉ

Afin d'accélérer le retour de peuplements forestiers de haute valeur économique et écologique après l'abandon de l'agriculture, on peut envisager l'afforestation avec les plantations d'arbres à croissance rapide. En plus de leur production ligneuse, ces plantations pourraient amener d'autres avantages, tels que la restauration écologique et/ou la culture de produits forestiers non ligneux en sous-bois. Pourtant, peu d'études ont comparé directement l'habitat créé par les plantations avec l'habitat forestier naturel créé par la succession. Dans une première étude nous avons comparé les effets des plantations avec la succession naturelle en champ abandonné (friches), en termes d'attributs abiotiques et des communautés végétales de sous-bois. Nous avons caractérisé les propriétés chimiques et l'humidité du sol, la lumière, la litière de feuilles, et les communautés végétales de sous-bois dans des plantations expérimentales de deux clones de peuplier hybride, dans des champs abandonnés et des forêts de seconde venue à proximité des plantations à huit sites dans la région des Cantons-de-l'Est, Québec, Canada. Les deux types de plantations n'ont pas eu d'effet significatif sur les propriétés chimiques des sols, comparés aux friches, mais elles avaient des sols plus secs que les friches et les forêts. Nous avons observé plus de litière de feuilles et moins de lumière dans les plantations du clone MxB que les plantations du clone DxN, tandis que les plantations les plus productives des deux clones étaient similaires aux forêts secondaires en terme de ces caractéristiques. Les plantations ont favorisé la colonisation des sites par les arbres, tandis que les communautés d'herbacées et d'arbustes sont demeurées similaires à celles des friches. Nous concluons que les plantations de peuplier hybride ont la capacité d'accélérer la restauration de certains attributs de sous-bois, particulièrement aux sites récemment abandonnés et productifs. Dans une deuxième étude nous avons utilisé des introductions expérimentales de plantes pour évaluer la valeur de l'habitat de sous-bois des plantations de peuplier hybride, en comparaison avec celui des forêts de seconde venue. Nous avons transplanté quatre espèces herbacées indigènes de sous-bois dans six plantations et dans des boisés avoisinants. Nous avons mesuré la survie, la taille, et la fleuraison immédiatement après la transplantation et un an plus tard. Trois espèces sur quatre (*Asarum canadense, Sanguinaria canadensis, Maianthemum racemosum*) ont eu autant ou plus de succès dans les plantations que dans les boisés, tandis que la tendance était l'inverse pour le trille blanc (*Trillium grandiflorum*). Bien que ces résultats soient préliminaires, ils suggèrent que la culture d'espèces de sous-bois dans les plantations de peuplier hybride pourrait représenter une alternative intéressante à leur culture dans les boisés, et surtout pour éviter toute récolte dans les populations naturelles. Globalement, ces résultats suggèrent que les changements apportés par les plantations au niveau de la lumière et de la litière sont suffisants pour favoriser la colonisation par les espèces d'arbres et le maintient du stade adulte de certaines espèces forestières herbacées. Par conséquence, le manque de colonisation spontanée des plantations par les espèces de sous-bois refléterait une limitation à un autre stade de leur cycle de vie. En somme, les plantations de peuplier hybride apparaissent prometteuses comme peuplements de transition au cours de l'afforestation, et pourraient être utilisées pour la restauration écologique ou la culture de produits forestiers non ligneux.

Mots clés : peuplier hybride, friche agricole, lumière, sol, sous-bois, produit forestier non ligneux

ABSTRACT

To accelerate the return of economically and ecologically valuable forest stands after the abandonment of agriculture, active afforestation using plantations of fast-growing tree species may be desirable. In addition to producing wood, these plantations could also serve other functions, such as ecological restoration and/or the cultivation of non-timber forest products in the understory. However, few studies have directly compared the habitat created by plantations to the natural forest habitat created through old field succession. In a first study, we compared the effects of plantations to old field succession in terms of abiotic attributes and understory vegetation communities. Soil chemical properties, soil moisture, light, leaf litter, and understory vegetation communities were sampled in experimental plantations of two hybrid poplar clones and in neighbouring unmanaged abandoned fields and older secondary forests at eight sites in the Eastern Townships region of Quebec, Canada. Neither plantation type had a significant effect on soil chemical properties compared to the abandoned fields, but both had drier soils than either the abandoned fields or the secondary forests. More leaf litter and denser shade was observed in the MxB plantations than in the DxN plantations, while the more productive plantations of both clones were similar to the forests in terms of these characteristics. Both plantation types favoured the colonization of the sites by tree species compared to the unmanaged fields, while the herb and shrub communities remained similar to those of the abandoned fields. We conclude from this study that hybrid poplar plantations of either clone can accelerate the restoration of certain understory attributes, particularly at recently-abandoned and productive sites. In a second study, we used experimental introductions to assess the habitat value of hybrid poplar plantations, compared to secondary forests. Four species of understory forest herbs were transplanted into plantations of two hybrid poplar clones and neighbouring woodlots at six sites. Survival, plant size, and flowering were measured just after transplantation and after one year. Three of the four species (*Asarum canadense*, *Sanguinaria canadensis*, *Maianthemum racemosum*) performed equally well or better in the plantations compared to the woodlots, while the opposite trend was observed for white trillium (*Trillium grandiflorum*). While these results are only preliminary, they suggest that cultivating forest understory species in hybrid poplar plantations could provide an interesting alternative to their cultivation in naturally regenerated woodlots, and especially to avoid any harvest from natural populations. Overall, the results of these studies show that the changes produced by hybrid poplar plantations in terms of light and leaf litter are sufficient to create a habitat suitable for tree species colonization and for the adult life stages of certain forest herb species. The failure of many understory species to spontaneously colonize the plantations therefore most likely reflects a limitation on colonization at some other stage of their life cycle. In conclusion, hybrid poplar plantations appear promising for use as transitional stands during afforestation, and for ecological restoration and/or non-timber forest product cultivation.

Keywords: hybrid poplar, abandoned farmland, light, soil, understory, non-timber forest product

CHAPTER I

GENERAL INTRODUCTION AND CONTEXT

1.1 Afforestation of abandoned farmland

Deforestation in North America and Europe for agriculture has resulted in the loss and fragmentation of forest habitats in many landscapes (e.g., Bélanger and Grenier 2002; Peterken 2000). In the case of southern Quebec, the original forest cover has been severely fragmented and degraded, with just over 50% of the land in the St. Lawrence valley currently forested, and less than 20% forest cover in eight regional county municipalities (Bélanger and Grenier 2002). In the Montérégie area, one of the most intensively cultivated landscapes of the entire region, only 27.3% of the land remains forested, and this area declined by 3.4% over the three-year study period (Soucy-Gonthier et al. 2003). Belanger and Gauthier (2002) found that in such areas of intense deforestation, forest habitats are significantly fragmented, since fragmentation increased dramatically below a threshold of 50% forest cover.

The trend of deforestation is accompanied by a more recent trend toward the abandonment of less productive agricultural land, presenting an opportunity for afforestation. Abandoned farmland has become a common feature in many landscapes of Europe and North America as a result of rural exodus to urban areas and changes in production systems and economic structures over the past half century that made it unprofitable to farm on the more marginal agricultural lands (Domon and Bouchard 2007; Le Houérou 1993; Poyatos et al. 2003; Roura-Pascual et al. 2005). In southern Quebec, abandoned farmland was estimated to occupy 17 567 ha in the Estrie region in 1999 and 23 500 ha in the Montérégie region in 2000 (Vouligny and Gariépy 2008).

In the absence of human intervention, abandoned fields undergo a natural process of succession spanning many decades, and eventually leading to the development of mature forest. In New Jersey, tall shrubs dominated an old field 20 years after abandonment (Pickett 1982). In the Upper St. Lawrence region of Quebec, many old fields developed a closed tree canopy with immature stems after approximately 20 to 40 years of abandonment, while others were still dominated by herbaceous vegetation and low shrubs after 20 years (Aubin et al. 2008; Benjamin et al. 2005). Thus, there is often a lag time of several decades between the abandonment of agriculture and the development of a tree canopy. In addition, the forestry potential of many post-agricultural stands in southern Quebec has been found to be inadequate without silvicultural interventions, with relatively few shade-tolerant, economically-valuable hardwood species colonizing the understory of early successional forests on abandoned fields (D'Orangeville et al. 2008; Truax et al. 2000).

To accelerate the return of economically and ecologically valuable forest stands after the abandonment of agriculture, active restoration may be desirable (Chazdon 2008). Forest restoration is most commonly approached through tree-planting. Objectives of plantation projects can include wood production, the provision of ecological services, such as carbon capture or stream bank stabilization, and/or the restoration of biological communities. These objectives need not be mutually exclusive; rather, a plantation can be designed to serve multiple functions (Paquette and Messier 2010).

Wood production is often of primary interest in plantations, due to its economic and social benefits. Thus, productive plantations can provide income to landowners, augment land values, contribute to rural development, and supply local industries. The enhanced development of the forestry industry in southern Quebec on abandoned farmlands could also contribute to a more diversified economy in rural communities that are struggling to stay afloat on agriculture alone (CAAAQ 2008; Coulombe et al. 2004). Active afforestation seems to be generally acceptable among landowners, who generally have no plans for these abandoned lands and are open to the idea of silvicultural improvements (Benjamin et al. 2007, 2008).

Intensive wood production is a key element of the TRIAD model for sustainable forest management, an increasingly influential model in North America (Coulombe et al. 2004; Côté et al. 2010). This model divides the territory into three land-use zones: a preservation zone, an ecosystem-based management zone, and an intensive production zone from which a large portion of the timber demands from the territory are to be met (Côté et al. 2010). Abandoned farmlands southern Quebec are ideal locations for intensive production, being accessible by a well-developed road network, with the most favourable climate in the province and often rich post-agricultural soils (Coulombe et al. 2004). The favourable conditions also allow plantations of fast-growing species such as hybrid poplar, which can reach a commercially harvestable size in as little as 15 to 20 years (Marchand and Masse 2007). Furthermore, the implementation of intensive plantations on abandoned farmland does not present the same ecological drawbacks as in natural forests, where the conversion to plantations can alter and simplify the existing forest ecosystems (Brockerhoff et al. 2008; Paquette and Messier 2010).

In addition to the timber value of plantations, the understory created by these trees could also be of interest as an environment for other plant species. As yet underdeveloped, this aspect of plantations could provide additional ecological and economic functions. One such example is the cultivation of horticulturally attractive native plant species as non-timber forest products. Native forest herb species are generally slow-growing and their harvest from wild populations is therefore often unsustainable (Charron and Gagnon 1991; Nantel et al. 1996; Nault and Gagnon 1993). Several understory species, including white trillium (*Trillium grandiflorum*), wild leek (*Allium tricoccum*), and bloodroot (*Sanguinaria canadensis*), are already listed as vulnerable in Quebec, due in part to risks of overexploitation of wild populations (Ministère du Développement durable, de l'Environnement et des Parcs du Québec 2010). Their cultivation in plantation understories could provide a more sustainable supply of these plants, as well as an additional and earlier return on investment for plantation owners.

Another potential function of plantation understories is the maintenance of forest biodiversity in the landscape. Since many species ranges are expected to shift as a result of climate change, the ability to quickly restore forest habitat connectivity may be of great value to

conservation efforts (Honnay et al. 2002; Paquette and Messier 2010). Fast-growing plantations could potentially serve such a restoration role, creating a shaded, forest-like understory environment that forest species could colonize spontaneously or in which ecological restoration projects could re-introduce populations of native shade-tolerant trees and forest herb species.

It should be mentioned that plantations have had a bad reputation from the point of view of biodiversity conservation, since many plantations are known to support little in the way of biodiversity (Brockerhoff et al. 2008; Paquette and Messier 2010). However, in evaluating the costs and benefits of plantations, it is most useful to compare them with the existing land-use at a given site (Brockerhoff et al. 2008; Paquette and Messier 2010; Stephens and Wagner 2007). In the context of plantations on degraded land such as abandoned farmland, the net impact for biodiversity is less clear, and may, in fact, be positive (Paquette and Messier 2010). Thus, in this thesis, we will compare plantations on abandoned farmland with a scenario of continued abandonment.

This thesis focuses on the potential of plantations on abandoned farmland to accelerate the creation of a forest-like understory environment, which may then be used for NTFP production, the restoration of forest understory communities, or as forested corridors between natural forest fragments.

1.2 Abiotic attributes of plantation understories

While a plantation can create tree cover on an old field very rapidly, it is important to understand whether the environment of a plantation understory is similar to that of a natural secondary forest, and whether a plantation understory can be as suitable for forest plant species as a secondary forest understory. Plantations may produce different environments as a result of site preparation disturbances, differences in tree species composition, reduced tree species diversity, and simplified structure.

In spontaneous old field succession, the typical progression from a herb-dominated community to a forest stand is associated with changes in soil characteristics (Hooker and

Compton 2003; Poulton et al. 2003; Richter et al. 1994), light availability (Dölle and Schmidt 2009), and vegetation community structure (Benjamin et al. 2005; Pickett 1982; Singleton et al. 2001). These characteristics determine the quality of the habitat for plant species colonizing the site and influence the competitive ability of species during different successional stages (Dölle and Schmidt 2009; Gleeson and Tilman 1990; Tilman 1987). In addition, the increase in soil carbon stocks commonly associated with reforestation (Hooker and Compton 2003; Richter et al. 1994; Robertson and Vitousek 1981; Thorne and Hamburg 1985) has important implications for climate change, given that soils represent the largest terrestrial organic carbon pool globally (Jobbágy and Jackson 2000).

Plantation establishment and growth is also associated with changes in environmental characteristics; however, these changes have been far less studied than successional changes, and the implications of such changes for native understory plant species are not clear. Studies of broadleaf tree plantations in broadleaf temperate forest zones have shown that such planted trees can have similar effects on the soil as they grow as the trees of secondary successional forests. The distribution of soil pH within a monospecific oak plantation in Eastern Europe was found to be similar to that of a secondary successional forest with similar sized trees, despite a somewhat simplified stand structure and lower tree species diversity (Bobiec 1998). Hardwood plantations were also found to increase the soil carbon and nitrogen contents over time (De Keersmaeker et al. 2004), which represents a similar trend to old field succession (Poulton et al. 2003; Robertson and Vitousek 1981). However, the disturbances associated with plantation establishment may in fact lower the soil carbon content initially, followed by increases in soil carbon as the planted trees grow (Laganière et al. 2010). Faster-growing tree species may cause a more rapid accumulation of soil carbon than slower-growing species (Laganière et al. 2010).

Forest floor and soil properties can be drastically different under conifer plantations than under the natural secondary forest in regions where the natural forest consists primarily of hardwood species. Such plantations create a litter layer dominated by conifer needles, which can negatively affect the establishment of native forest plant species that are adapted to a deciduous broadleaf litter substrate (Aubin et al. 2008; Dzwonko 2001). Coniferous litter also differs from that of the natural forest in terms of decomposability and chemical

properties, resulting in a lower soil pH and lower concentrations of calcium, magnesium, and potassium, compared to natural hardwood forests (Dzwonko 2001; Fahy and Gormally 1998).

Light levels in the understory are also affected by overstory composition and structure. Coniferous plantations often cast denser shadows than deciduous hardwood plantations, and there are reports of near-total elimination of vascular understory vegetation by dense conifer plantations after full canopy closure (Ferris et al. 2000; Summers et al. 1999). In one study, the denser tree spacing within plantations of several conifer species was cited as one of the primary factors causing the development of a very different understory vegetation community from that of old-growth pine forests (Summers et al. 1999). When adequately spaced, however, plantations can create suitable understory light environments for native forest species. Thinning can also increase the habitat value of older plantations by forest herb species by increasing understory light levels (Ferris et al. 2000).

1.3 Understory vegetation communities in plantations

Certain plantations in the tropics have been cited as having the potential to support local vegetation and to accelerate the transition from field to forest-like environment (Mansourian et al. 2005; Parrotta et al. 1997). Research in the tropics has shown that plantations on old fields or degraded lands can indeed, under certain circumstances, have positive impacts on biodiversity by accelerating the reforestation process compared to the natural successional process (Mansourian et al. 2005; Parrotta et al. 1997). This research has elucidated several important potential functions of plantations in the reforestation of former agricultural land: plantations can act as "nurseries" for native forest plant species by creating a forest-like microclimate in the understory, shading out fast-growing open-field competitor species, promoting the development of a humus layer in the soil, and attracting seed-dispersing wildlife (Brockerhoff et al. 2008; Cole et al. 2010; Parrotta et al. 1997). However, several tropical and sub-tropical tree species have been reported to have allelopathic effects on understory vegetation, thus inhibiting the development of a diverse understory (Batish et al. 2001; Souto et al. 2001).

In the temperate zone, we know of only two studies that compare plantation understory communities to those of natural secondary forests originating from old-field succession. Aubin et al. (2008) compared the vegetation under deciduous plantations to the vegetation under deciduous post-agricultural forests of the same stage of canopy development in southern Quebec. In terms of functional groups, the vegetation under unplanted stands tended to be more characteristic of later-successional communities than the vegetation under the plantations. However, the unplanted stands also tended to be older than the plantations at a given canopy development stage, allowing more time for dispersal. Since many forest plant species have slow dispersal rates, dispersal could be an important factor in limiting the development of forest-like understory communities (Brunet and Von Oheimb 1998; De Keersmaeker et al. 2004; Singleton et al. 2001), especially at sites with no nearby seed sources (Dzwonko and Loster 1992; Matlack 1994).

The second study was in northern Quebec, in 8- to 30-year-old jack pine plantations, which were compared to the natural successional vegetation on old fields of a similar age, after 10 to more than 20 years since abandonment, which had yet only a few trees and had not yet reached the closed canopy stage (Gachet et al. 2007). In this case, the plantations apparently failed to accelerate the development of understory vegetation communities; however, like the previously described study, it was not possible to determine whether the lack of a forest-like understory community was due to an unsuitable environment within the plantation or to dispersal limitation on the part of understory forest plants.

Experimental introductions have been used to directly test the suitability of plantation environments as habitat for forest herb species. This approach provides a combined measure of all aspects of the understory habitat (including light and soil properties). It also overcomes the limitations of studying existing vegetation communities, which are often strongly influenced by dispersal (Brunet and Von Oheimb 1998; Singleton et al. 2001). After experimental introductions of forest herbs into 10-year-old mixed-species hardwood plantations, the introduced species performed as well or better in the plantations than in natural old-growth forests (Verheyen and Hermy 2004). This study also found no evidence of increased competition from ruderal species within the plantations (Verheyen and Hermy

2004). However, a longer-term study over the entire life cycle of the introduced plants would provide better evidence of habitat quality for these species.

Other studies of the understory vegetation in old-field plantations have shown effects of site preparation intensity, with more intense preparations resulting in a higher abundance of early successional species (Jeffries et al. 2010; Soo et al. 2009). These effects were observed seven to eight years after establishment in hybrid poplar plantations in Estonia (Soo et al. 2009) and lasted up to two decades in third-rotation loblolly pine plantations in North Carolina (Jeffries et al. 2010). The effects of site preparation are expected to be more important on longer-abandoned fields or in later rotations, when the vegetation has had more time to undergo succession.

Taken together, these multiple lines of evidence support the hypothesis that certain plantations can serve as suitable habitat for a variety of forest plant species, and that this habitat is potentially of as good quality for forest species as the habitat in natural secondary forests. Moreover, this habitat seems to develop in less time than through natural succession, even if forest understory species are slow to recolonize. By directly planting fast-growing trees onto an abandoned field, plantations are hypothesized to accelerate the transition of many environmental characteristics from open field to forest understory. This effect should diminish, however, the longer the lag time between agricultural abandonment and plantation establishment.

1.4 Objectives

The objectives of this thesis are (1) to evaluate the effects of the establishment and growth of hybrid poplar plantations on understory environmental characteristics, compared to unplanted old fields and secondary forests; (2) to assess the colonization of hybrid poplar plantations by forest understory species and tree seedlings; and (3) to perform a preliminary assessment of the habitat quality of hybrid poplar plantations for four species of native understory herbs by way of a transplant experiment.

The results of this study will be of value for land-use planning, which must increasingly accommodate a number of objectives brought forward by land-owners and the general public. Knowledge of the understory environments within hybrid poplar plantations is a step toward developing new models of multi-functional plantations. The multiple functions considered in this project are non-timber forest product cultivation and restoration of forest understory communities, in addition to wood production.

CHAPTER II

CAN HYBRID POPLAR PLANTATIONS ACCELERATE THE RESTORATION OF FOREST UNDERSTORY ATTRIBUTES ON OLD FIELDS?

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Abstract

Multi-functional plantations using fast-growing tree species can potentially be used to accelerate the restoration of forest habitat on abandoned farmland. However, few studies have directly compared the effects of active afforestation using plantations to natural afforestation through old field succession. The present study compares the effects of the establishment and the first ten years of growth of two different hybrid poplar clones to old field succession in terms of abiotic attributes and understory vegetation communities. Experimental hybrid poplar plantations were established in 2000 on old fields abandoned at different times at eight sites in southern Quebec, Canada. After ten years, soil chemical properties, soil moisture, light, leaf litter, and understory vegetation communities were sampled in the plantations and in neighbouring unmanaged abandoned fields and secondary forests. Neither type of plantation had any significant effect on soil chemical properties compared to the abandoned fields, but both had drier soils than either the abandoned fields or the secondary forests. More leaf litter and denser shade was observed in the MxB plantations than in the DxN plantations, while the more productive plantations of both clones were similar to the forests in terms of these characteristics. The plantations favoured the colonization of the sites by tree seedlings and saplings compared to the unmanaged fields, producing a nurse-stand effect. In contrast, the herb and shrub communities under the plantations remained similar to those of the abandoned fields. More research is needed to directly assess the quality of plantation habitats for native understory plants and the relative importance of dispersal limitations. In conclusion, hybrid poplar plantations appear to be capable of accelerating the restoration of certain understory attributes, and these accelerating effects were most apparent at recently-abandoned sites with high hybrid poplar productivity. The nurse-stand effect on tree colonization represents a promising new avenue for combining fibre production with forest restoration.

Keywords: hybrid poplar plantations, afforestation, abandoned farmland, understory, soil, light, leaf litter, community, nurse stand, restoration

2.1 Introduction

Deforestation in North America and Europe for agriculture has resulted in the loss and fragmentation of forest habitats in many landscapes (e.g., Bélanger and Grenier 2002; Peterken 2000). The trend of deforestation is accompanied by a more recent trend toward the abandonment of less productive agricultural land, presenting an opportunity for afforestation. Abandoned farmland has become a common feature in many landscapes of Europe and North America as a result of rural exodus to urban areas and changes in production systems and economic structures over the past half century that made it unprofitable to farm on the more marginal agricultural lands (Domon and Bouchard 2007; Le Houérou 1993; Poyatos et al. 2003; Roura-Pascual et al. 2005).

In the absence of human intervention, abandoned fields in northeastern North America undergo a natural process of succession, generally leading to the development of a forest stand within a few decades. For example, in the Upper St. Lawrence region of Quebec, many old fields developed a closed tree canopy after approximately 20 to 40 years of abandonment, while others were still dominated by herbaceous vegetation and low shrubs after 20 years (Aubin et al. 2008; Benjamin et al. 2005). However, without silvicultural intervention, the forestry potential of post-agricultural forests in southern Quebec has been found to be inadequate, with relatively few shade-tolerant, economically-valuable hardwood species colonizing the understory of early successional forests on abandoned fields (D'Orangeville et al. 2008; Truax et al. 2000).

To accelerate the return of economically and ecologically valuable forest stands after the abandonment of agriculture, active restoration through tree planting may be desirable (Chazdon 2008). Objectives of plantation projects can include wood production, the provision of ecological services such as carbon capture or stream bank stabilization, and/or the restoration of biological communities. Restoration objectives can potentially be combined with wood production objectives in multi-functional plantations (Paquette and Messier 2010). Fast-growing tree species could be especially interesting in such projects, creating a shaded, forest-like understory environment that forest species could colonize or into which ecological restoration projects could re-introduce populations of native shade-

tolerant trees and forest herb species. Since many species ranges are expected to shift as a result of climate change, the ability to quickly restore forest habitat connectivity may be of great value to conservation efforts (Honnay et al. 2002). Native tree species are more suitable in this role (Paquette and Messier 2010; Stephens and Wagner 2007), and hardwood species should be preferred over conifers for plantations in the hardwood forest zone of southern Quebec (Aubin et al. 2008).

Hybrid poplars are shade-intolerant trees that grow extremely rapidly on favourable sites, and which are commonly planted in North America and Europe for wood fibre production. Despite the fact that many commonly-planted clones originate from one or more exotic species, hybrid poplar plantations can nevertheless provide ecological services such as carbon capture and non-point source pollution abatement in agricultural settings (Fortier et al. 2010b). On the other hand, the impacts of hybrid poplar plantations on soil characteristics and understory environmental attributes are not well understood. Hybrid poplar clones with different parent species may also produce different effects, with previous studies noting differences among species in terms of allocation of biomass to branches and leaves (Fortier et al. 2010a), root density (Fischer et al. 2006), nitrogen cycling (Schimel et al. 1998) and understory vegetation biomass (Fortier et al. 2011).

In old field succession, the typical progression from a herb-dominated community to a forest stand is associated with changes in soil characteristics (Hooker and Compton 2003; Poulton et al. 2003; Richter et al. 1994), light availability (Dölle and Schmidt 2009), and vegetation community structure (Benjamin et al. 2005; Pickett 1982; Singleton et al. 2001). On the other hand, the changes associated with plantations, especially hybrid poplar plantations, are less well understood.

Soil carbon stocks have been found to increase over time in both old field succession and plantation development (Hooker and Compton 2003; Laganière et al. 2010; Richter et al. 1994; Robertson and Vitousek 1981; Stevens and van Wesemael 2008; Thorne and Hamburg 1985). However, in plantations, the disturbances associated with plantation establishment may in fact lower the soil carbon content initially, followed by increases in soil carbon as the

planted trees grow (Laganière et al. 2010). Faster-growing tree species may also cause a more rapid accumulation of soil carbon than slower-growing species (Laganière et al. 2010).

The distribution of soil pH within a monospecific oak plantation in Eastern Europe was found to be similar to that of a secondary successional forest with similar sized trees, despite a somewhat simplified stand structure and lower tree species diversity (Bobiec 1998). Hardwood plantations were also found to increase the soil carbon (C) and nitrogen (N) contents over time (De Keersmaeker et al. 2004), which represents a similar trend to old field succession (Poulton et al. 2003; Robertson and Vitousek 1981).

We know of only two studies that compare plantation understory vegetation communities to those of forest stands originating from old field succession. Aubin and colleagues (2008) compared the vegetation under deciduous plantations to the vegetation under deciduous post-agricultural forests of the same stage of canopy development in southern Quebec (Aubin et al. 2008). In terms of functional groups, the vegetation under unplanted stands tended to be more characteristic of later-successional communities than the vegetation under the plantations. However, the unplanted stands also tended to be older than the plantations at a given canopy development stage, allowing more time for dispersal. In the second study, Gachet and colleagues found that the vegetation under 8- to 30-year-old jack pine plantations in northern Quebec was similar to the natural successional vegetation on old fields of a similar age (Gachet et al. 2007).

Dispersal may be a limiting factor in the development of forest understory communities in both plantations and secondary forests (Brunet and Von Oheimb 1998; De Keersmaeker et al. 2004; Singleton et al. 2001). On the other hand, many studies have failed to find an effect of dispersal mode on colonization success, although this could be due in part to imperfect dispersal classification schemes (Flinn and Vellend 2005).

In plantations, site preparation and silvicultural activities may also favour early successional species and hinder the development of late successional understory communities (Aubin et al. 2008; Jeffries et al. 2010; Soo et al. 2009). The negative effects of site preparation are expected to be more important on longer-abandoned fields and in later rotations, when the vegetation has had more time to develop.

The present study evaluates the effects of the establishment and first ten years of growth of hybrid poplar plantations of two contrasting clones on abandoned farmland, in terms of both abiotic attributes and understory vegetation communities. The study made use of eight experimental 10-year-old hybrid poplar plantations, established on old fields or pastures of various elevations, soil richness, and ages since abandonment. The objectives of this study were (1) to compare the abiotic attributes in plantations of two clones of hybrid poplar to those of unplanted environments of similar land-use history (abandoned fields or pastures) or of similar canopy development (older secondary forest), and (2) to assess the colonization of the plantation understories by native forest herbs, shrubs and tree seedlings.

2.2 Methods

2.2.1 Study area and plantation sites

The study took place in the Eastern Townships region of Quebec, Canada (Fig. 2.1), across a regional climatic gradient corresponding to an elevation gradient from the St. Lawrence Lowlands to the foothills of the Appalachian Mountains. This gradient spans three ecological regions: region 1a-T, at the lowest elevetations and with the mildest climate, with typical mature forest stands on mesic sites is being dominated by sugar maple and hickory (*Acer saccharum* - *Carya cordiformis*); region 2c-T, at mid-elevations, characterized by sugar maple - basswood (*Acer saccharum* - *Tilia americana*) stands; and finally region 3d-M, at the highest elevations, characterized by sugar maple - yellow birch (*Acer saccharum* - *Betula alleghaniensis*) stands. The landscapes of southern Quebec represent an excellent opportunity to study the multi-functional potential of tree plantations. Many regions have been largely deforested due to agriculture; however, agricultural activities have more recently been concentrated in the St. Lawrence Lowlands, resulting in the abandonment of many fields outside this region (Domon and Bouchard, 2007).

The present study uses a series of similar experimental hybrid poplar plantations, planted in May 2000 for a study on hybrid poplar establishment and growth at eight sites across the Eastern Townships (Truax and Gagnon, 2008). The site characteristics are summarized in Table 2.1. The plantations were all established on privately-owned fields that had been used

for either grazing or crops, and subsequently abandoned. The vegetation before planting ranged from herbaceous to mixed herbaceous - shrub communities. Sites were prepared for planting in the fall of 1999 by ploughing and disking, and resprouting or germinating vegetation was eliminated in June 2000 by an application of glyphosate herbicide over the entire plantation area. Following this treatment, 2 m long rooted cuttings of nine different hybrid poplar clones were planted by hand at each site at a stem density of 833 ha^{-1} (4 m between rows and 3 m between stems along the row). Glyphosate was again applied in June 2001, but only between the rows.

After 10 seasons of growth, a wood volume production gradient had emerged across the sites. At certain sites, the plantations showed exceptional growth, while at others, they showed average or poor growth. The majority of these plantations had, however, developed a closed canopy. The understory environments of these plantations were assessed during the 10^{th} growing season (summer 2009) by comparing them with neighbouring abandoned fields and naturally-regenerated secondary woodlots at each site.

2.2.2 Study design

The plantations consisted of three adjacent blocks of 36 m x 36 m aligned in the direction of the slope. Each block was divided into nine 12 m x 12 m plots, to which nine hybrid poplar clones were randomly assigned. Each plantation contained three replicate plots of each of the nine clones. Two of these clones were chosen for the present study, both of which are hybrids of one native and one exotic parent species, developed in Quebec: clone 915303, a hybrid of *Populus maximowiczii* and *P. balsamifera* (M x B), and clone 131, a hybrid of *P. deltoides* and *P. nigra* (D x N). These two clones were selected due to their clear differences in leaf biomass and branching patterns. At three of the eight sites, where clone 131 showed significant damage, one or two plots of clone 3333, another D x N hybrid, were used as replacements. At each site, we used three 12 m x 12 m plots of MxB hybrid poplar and three 12 m x 12 m plots of DxN hybrid poplar.

Abandoned field areas were sampled at each site as controls, for comparison with the plantation environments. These field areas consisted of unplanted portions of the same

abandoned fields on which the hybrid poplar plantations had been established, and were similar to the land under plantation in terms of land-use history, drainage, slope, etc. Herbaceous to mixed herb-shrub vegetation covered these abandoned field areas, with a few trees beginning to establish themselves on some sites. At three sites (Bromptonville, St-Adrien, and La Patrie), other species of hardwood or coniferous trees had been planted in the abandoned fields with minimal site preparation, and had reached a maximum of 8.2 cm diameter at breast height by 2009, with total basal area less than 2.06 m^2/ha. It was therefore assumed that these trees had not yet had significant effects on the environment (vegetation and soils). At each site, three 12 m x 12 m plots were established within these abandoned field areas, wherever possible aligned with the three blocks of the plantations.

Areas of hardwood-dominated secondary forest were also sampled at each site as a second set of controls, referred to henceforth as woodlots. These woodlot areas had regenerated naturally after either the harvest of a previous stand, or the abandonment of agriculture, and varied in terms of drainage, stand maturity and canopy composition (see Appendix A). The age of each stand was estimated based on cores taken from a sample of the largest trees and interviews with landowners. Three 12 m x 12 m plots were selected from within these stands, located as near as possible to the plantations. Exceptionally, at the La Patrie (LAP) site, the three woodlot plots were located 3.6 km from the plantation.

Thus, 96 plots were sampled in all from the hybrid poplar plantations, abandoned fields, and woodlots (8 sites x 4 environments (2 clones, field, woodlot) x 3 replicates).

2.2.3 Soil characteristics

Within each of these 96 plots, we collected five soil samples distributed systematically within the plot for chemical analysis. Samples were taken from the mineral soil at a depth of between 5 cm and 10 cm, between July 15 and August 6, 2009. This depth corresponds to the principal rooting zone of herbaceous plants and tree seedlings. The five samples from each plot were combined into one, then air-dried and passed through a 2 mm sieve. The pH was measured in a suspension of one part soil in two parts distilled water. The available potassium (K), calcium (Ca), and magnesium (Mg) contents were determined through

extraction with $BaCl_2$ and detection by atomic absorption. The extractable phosphorus (P) content was measured using the Bray-2 method (Bray and Kurtz 1945) (modified by F. Lambert). Total N and total C were measured using dry combustion at 960°C, high-temperature reduction of the combustion products, and thermo-conductometric detection using a multi-elemental analyzer (vario MACRO, Elementar Analysensysteme GmbH, Hanau, Germany).

Soil moisture was sampled twice during the growing season, between June 23 and 26, 2009 and between August 14 and 15, 2009, corresponding to dry periods with no significant rainfall events recorded in the 48 hours prior. Samples were collected at a depth of 10 cm, one from the centre of each plot, in small metal containers. The moisture content was then determined gravimetrically after oven drying for 72 hours at 60°C.

2.2.4 Other environmental characteristics

The light availability was measured once in each plot between July 15, 2009 and August 3, 2009 on an overcast day or when the sun was at a low angle. A digital hemispheric photo was taken at the plot centre at a height of 90 cm and oriented vertically toward the sky or canopy. Photographs were analyzed using the Gap Light Analyzer software, v. 2.0 (Frazer et al., 1999), to determine canopy openness and the average light received during the growing season.

Leaf litter biomass was measured between October 26, 2009 and November 4, 2009, after almost all the leaves had fallen from every tree. The leaf litter was collected from a 50 cm x 50 cm microplot at the centre of each plot and subsequently dried and weighed.

2.2.5 Vegetation

The vegetation in each of the 96 plots was recorded between July 7, 2009 and August 5, 2009. Subplots of 7 m x 8 m, fully contained within the 12 m x 12 m plots, were used for the recording of the herb and shrub layer vegetation. All vascular plants were identified to

species to the extent possible, except for *Salix* spp., *Amelanchier* spp., and *Viola* spp. The percent cover of herbaceous and shrub species was visually estimated over the entire subplot. The total percent cover of the herb/shrub layer was also estimated in each plot. Tree seedlings (height < 1.3 m) were counted.

Tree communities were also described for each plot during the 2009 growing season, between August 6 and September 25, over the entire 12 m x 12 m plot. The diameter at breast height (DBH) was measured for all trees (DBH ≥ 10 cm) and saplings (height > 1.3 m and DBH < 10 cm). The DBH of each of the planted hybrid poplars was also measured at the end of the growing season, between September 10 and 25, 2009. Root suckers of hybrid poplar trees were also measured accordingly.

2.2.6 Analysis

Stand basal area was calculated for each plot, including all trees and saplings. The importance of the natural regeneration in each plot of *Acer rubrum*, *Fraxinus* spp., and *Betula* spp., as well as all tree species combined, was compared using an abundance index, calculated as:

$$\text{Abundance index} = \text{Number of saplings/ha} + (1/10 * \text{Number of seedlings/ha})$$

The coefficient of 1/10 was chosen to reflect the presumed increased importance of saplings toward the future canopy compared to seedlings.

A Shannon diversity index was calculated for the herb/shrub layer of each plot, excluding tree species (Shannon and Weaver 1949). Total cover was also calculated for the herb/shrub layer, as the sum of the percent covers of all herb and shrub layer species, and for the shrub layer only, as the sum of the percent covers of all species for which the USDA Plants database (USDA, NRCS 2011) lists "shrub" as one of the possible growth habits. The native status of each species was obtained from the VASCAN database (Brouillet et al. 2010). The relative abundance of introduced species was then calculated as the sum of the relative percent cover of all introduced species in a given plot.

A series of analyses of variance (ANOVA) was used to evaluate the effects of the hybrid poplar plantations on each measured soil attribute, the stand basal area of trees, canopy openness, light transmitted through the canopy, leaf litter biomass, the seedling-sapling abundance indices, herb and shrub layer diversity, the total cover of the herb/shrub layer and of shrubs, and the relative cover of introduced species. The model for each test included treatment (four levels: 2 hybrid poplar clones + 1 abandoned field control + 1 natural forest control), site, and treatment-site interaction as fixed effects. Response measures were subjected to log, arcsine-root, or Box-Cox transformations if the normality of ANOVA residuals and homoscedascicity were improved by doing so. Since the stand basal area varied considerably among sites and treatments, and since we hypothesized that stand basal area is an important factor controlling many other abiotic and biotic variables, we investigated these relationships using simple linear regressions. We summarized the relationship between environmental variables with a principal components analysis (PCA), after log-transforming the data for all soil nutrients, stand basal area, canopy openness, litter, soil moisture, and seedling abundance. To compare understory communities within the four environments, we also performed a detrended correspondence analysis (DCA) on understory species relative abundance (percent cover or seedling-sapling abundance index), and subsequently fitted measured abiotic and biotic variables to this ordination. All ANOVAs and regressions were done using JMP (SAS Institute, Cary, NC), and ordinations were done using the vegan package in R (Oksanen et al. 2010).

2.3 Results

2.3.1 Site and environment effects

Significant site effects were detected for all 22 measured variables (Table 2.2). For most variables, a significant effect of the type of environment (abandoned field, woodlot, DxN poplar or MxB poplar) was also detected, and this effect was highly significant for all canopy and litter variables. Out of the 22 variables analyzed, F-values were highest 13 times for environment effects and 9 times for site effects. The interaction between site and

environment was also significant for all variables except June soil moisture, but in most cases (17 out of 22) it was less important than the main effects.

2.3.2 Soil properties

After ten seasons of growth, we observed no overall effects of the hybrid poplar plantations on any soil chemical property, when compared with the abandoned field controls (Table 2.3). At the individual site level, only a few significant differences were found between the plantations and fields: at one site, the MxB poplar plantations had a lower pH and lower soil Ca concentrations than the abandoned field and at another site, the DxN poplar plantation had a lower P concentration than the field. In contrast, the woodlot soils were generally distinct from those of the other three types of environments, being on average more acidic, with higher carbon contents, higher C:N ratios, and higher concentrations of N, K, and Mg (Table 2.3). However, the differences in soil properties between the woodlots and the plantation/field environments were not consistent across all sites and at some sites the relationships were opposite those of the general trends. For example, the pH of the woodlot soils was quite variable among the eight sites, and at the Bedford site was as high as pH 6.12, significantly closer to neutral than the plantation and field soils (Fig. 2.2). Similarly, the soil Mg concentrations were more variable in the woodlots than in the fields and plantations, resulting in lower Mg concentrations in the woodlot soils than in the other soils at certain sites (Fig. 2.2). These types of variations among the sites were reflected in relatively small, but significant, interaction effects for all soil chemical properties (Table 2.2).

In contrast to the chemical properties, the plantation soils showed a difference from the abandoned field soils in terms of humidity, with both types of plantations having on average significantly drier soils than either the abandoned fields or the woodlots during a dry period in August (Table 2.3). This pattern was consistent across all sites but one, but was too small to be detected at any one site, except at La Patrie where the abandoned field was particularly wet (Fig. 2.2). For the measurements in June, the same trends were apparent, but the difference between the plantations and the abandoned fields was not significant (Table 2.3). There was also an effect of basal area among the poplar plantations, with the more productive

plantations being associated with drier soils, after the effect of elevation was partialled out ($r = -0.595$; $p < 0.001$ for the partial correlation). A particularly dry abandoned field at the St-Adrien site and a particularly wet field at the La Patrie site (Fig. 2.2) contributed to a small but significant interaction effect for August humidity and a close to significant interaction effect ($p = 0.064$) for June (Table 2.2).

Overall site effects were also highly significant for all soil properties (Table 2.2). The higher elevation sites tended to have more humid soils with higher concentrations of P and N, and higher C:N ratios (see Fig. 2.2 for soil humidity). For many variables, however, the differences between sites did not follow the elevation gradient (see Fig. 2.2 for examples with pH and Mg).

2.3.3 Canopy and litter attributes

The most noticeable effects of the plantations on the local environment were the canopy and litter effects (Table 2.3). Compared to the abandoned fields, both types of poplar plantations had significantly higher stand basal areas, with reduced canopy openness, reduced solar radiation beneath the canopy, and increased leaf litter biomass (Table 2.3). However, the plantations were still on average well behind the woodlots in terms of these characteristics, except in the case of litter production in the MxB poplar plantations (Table 2.3). The two types of hybrid poplar plantations had on average similar stand basal areas, but the MxB plantations had significantly lower canopy openness and light levels, and more leaf litter (Table 2.3). The variability observed in canopy openness, light, and litter among the plots can be in large part explained by differences in basal area ($r^2 = 0.811$, 0.759, and 0.710 respectively; Fig 2.3 for light and litter). No systematic difference is apparent between the plantations and the woodlots in terms of either light levels or litter biomass beyond the difference that is explained by the stand basal areas (Fig. 2.3). The size of the hybrid poplars and the degree of canopy development was quite variable among the sites, so that at certain sites (e.g., Bedford and Bromptonville) the plantations equalled or surpassed the woodlots in terms of stand basal area, canopy closure, shading, and litter, while at other sites (e.g., Stornoway) the plantations had canopy and litter attributes more similar to those of the fields.

The woodlots were also variable, showing differences in tree sizes and stem density among the sites. These site differences contributed to the significant site and interaction effects observed for all of these variables, though in all cases environment remained the overwhelming effect (Table 2.2).

2.3.4 Understory vegetation

The hybrid poplar plantations contained significantly more tree seedlings and saplings than the abandoned fields (Table 2.3), reflecting primarily an increase in abundance of *Betula alleghaniensis* and *Fraxinus* spp. However, the plantations still contained approximately four times fewer seedlings and saplings than the woodlots, including significantly fewer *Fraxinus* spp. and *Acer rubrum* (Table 2.3). Although the plantations and the fields contained greater mean abundances of *Betula* spp. than the woodlots, this was primarily due to the especially high abundance of these seedlings and saplings in the plantations and fields of the St-Adrien site, and was not significant overall. There were also significant differences between the sites in terms of overall seedling-sapling abundance (Table 2.2), with the St-Adrien and Melbourne sites containing far more seedlings and saplings than the others, mainly *Fraxinus* spp. and *Betula* spp. (Fig 2.2). The sites also varied in terms of the degree of difference in seedlings-sapling abundance between the woodlots and the other three environments (the interaction effect, Table 2.2); however, at each site the abundance of seedlings and saplings was highest in the woodlots (Fig 2.2). Differences in stand basal area explained 26.8% of the total variance in seedling and sapling abundance; however, at similar basal areas, the woodlots tended to contain more seedlings and saplings than the plantations (Fig 2.4).

The cover of the herb and shrub layers of the plantations was lower than in the abandoned fields (Table 2.3). While the herb and shrub layer beneath the DxN poplar plantations was only slightly sparser than that of the field (mean total cover = 203% vs. 256%), the MxB plantations had a more important impact on the herb and shrub layer cover (mean cover = 163%), although the cover was still significantly higher than that of the woodlots (mean cover = 93%). The effect of the type of environment was the dominant effect for this

variable, but site and interaction effects were also significant (Table 2.2), reflecting in part differences in stand basal area ($r^2 = 0.488$; Fig. 2.4). There was also an apparent effect of the hybrid poplar clone, beyond the effect of basal area: at stand basal areas greater than 20 m^2/ha, the DxN poplar plantations had higher herb and shrub layer covers than most of the MxB poplar plantation and woodlot plots (Fig. 2.4).

No significant differences were detected between the plantation and abandoned field communities in terms of Shannon's diversity index or the relative abundances of either shrubs or introduced species (Table 2.3). The herb and shrub layers of the woodlots, on the other hand, were generally distinct from those of the other three environments, being more diverse, containing a lower relative abundance of introduced species, and a higher abundance of shrubs (Table 2.3). The woodlot communities were not, however, significantly more diverse than the communities beneath the MxB poplars and did not contain significantly more shrubs than the DxN poplar plantations. The diversity of the vegetation varied significantly by site and the interaction effect was also significant (Table 2.2); at most sites the woodlots were the most diverse environment while the relationship between the other three environments varied. The site and interaction effects for shrub cover are shown in Figure 2.2. Site effects are the most important for explaining the variability in shrub abundance (Table 2.2), with overall higher shrub covers at the Ste-Catherine, St-Adrien, Melbourne, and Stornoway sites (Fig. 2.2). At the Melbourne and Stornoway sites, the shrub cover tended to be lower in the plantations compared to the fields and woodlots (Fig. 2.2). At the Ste-Catherine site, on the other hand, a trend can be observed toward higher abundances of shrubs in the plantations than in the fields, largely due to the high abundance of the invasive shrub *Rhamnus frangula* in certain areas of the plantation (Fig. 2.2). The site effect was also important in explaining the relative abundance of introduced species (Table 2.2), with the Ste-Catherine site having the highest abundance as a result of the invasion by *Rhamnus*. The relative importance of invasive species at the other sites appeared to be correlated with human population density, although this was not quantified. At every site, the relative importance of introduced species was lowest in the woodlots.

2.3.5 Multivariate analyses

To investigate the associations between the many abiotic and biotic attributes described above, a principal components analysis (PCA) was done on a subset of these variables (Fig 2.5). The first two axes explained 45.7% of the variability in the dataset. The first axis appears to be a successional gradient associated with increasing stand age and changes in soil chemistry (increasing acidity), canopy effects (stand basal area, shading and litter), and understory vegetation (increasing seedling-sapling abundance, decreasing abundance of introduced species and decreasing herb and shrub layer cover). Basal area is tightly coupled with litter, light, and herb/shrub layer cover along both the first and second axes, forming a distinct canopy development gradient, which is largely independent from age, soil chemical properties, and community composition attributes. Age remains associated with increasing acidity, C:N ratio, and seedling-sapling abundance and decreasing abundance of introduced species along both the first and second axes. An elevation gradient is also apparent along the second axis, correlated with increasing shrub cover, soil humidity and soil N and C:N ratios, and decreasing soil P concentrations. Differences between the environments were detected along the first and second axes ($F_{3,92}$ = 121.90; $p < 0.001$ and $F_{3,92}$ = 6.1554; $p = 0.001$, respectively). The woodlots were situated at the positive end of the first axis and were distinguished from the plantations most clearly along the stand age gradient. The abandoned fields, on the other hand, are situated closest to the negative end of the first axis, and were distinguished from the plantations along the canopy development gradient. The two types of plantations, however, were not significantly different from each other in terms of either of the first two PCA axes ($F_{1,46} = 2.63$; $p = 0.112$ and $F_{1,46} = 0.33$; $p = 0.567$).

The first two axes of the detrended correspondence analysis (DCA), showing the differences in community composition in each plot (herbs, shrubs, and tree seedlings/saplings), are shown in Figure 2.6. Fitting environmental variables to the ordination showed that the first axis represented the same successional gradient that characterized the first axis of the PCA, while the second axis represented the elevation gradient (Fig 2.6). There was a significant effect of environment on community composition along the first axis ($F_{3,92}$ = 83.768; $p <$ 0.001), with the woodlots being distinct from the other three types of environments. The MxB poplar plantation also showed an overall small, but significant, difference in

composition from the abandoned fields, indicating that after ten years the vegetation communities in these plantations had begun to respond to the changes in the environment. The effect of the plantations in shifting the species composition toward that of a forest understory was generally stronger in the more productive plantations. Only the four most productive plantations showed any real shift in vegetation toward the woodlots, the MxB poplar plantations showing a slightly greater shift than the DxN plantations, while at the Stornoway site, where the plantation canopy was the least developed and where the field had been abandoned the longest, the species composition in the plantations was actually less similar to the woodlots than was the vegetation in the abandoned fields. The separation between the plantations and the abandoned fields was much less distinct in this ordination, which was based on community composition, than in the PCA, which was based on environmental characteristics. No difference between environments was detected along the second axis ($F_{3,92} = 0.520$; $p = 0.669$).

2.4 Discussion

2.4.1 Abiotic and canopy attributes

In the absence of human intervention, abandoned farmland generally follows a pattern of environmental changes associated with changes in the vegetation through old field succession. These changes include a reduction in light availability (Dölle and Schmidt 2009), soil acidification (Richter et al. 1994), the accumulation of soil carbon and nitrogen (Hooker and Compton 2003; Poulton et al. 2003; Thorne and Hamburg 1985), and an increase in the soil C:N ratio. As expected, this pattern was reflected in the present study in the overall differences between the woodlots and abandoned fields.

At the site level, the woodlots were quite variable in terms of soil chemical properties, and the difference between the woodlots and the abandoned fields is not consistent across all sites. This may be due to differences in land-use history between the old fields and the woodlots, with differences in past clearing, ploughing, liming, fertilization, and/or grazing influencing the present-day properties of these soils. There is also a land-use bias that has operated historically in northeastern North America, in which marginal land, characterized by

poor soils, poor drainage, or steep slopes, tended to be abandoned earlier and has since returned to a forest cover (Domon and Bouchard 2007; Foster 1992; Glitzenstein et al. 1990). This bias operates not only at the regional/landscape scale, but also at the property-scale, possibly playing an important role in determining which areas of the sites in this study were abandoned early and have since become woodlots, and which areas were maintained under cultivation or pasture until more recently.

The hybrid poplar plantations in this study failed to accelerate any of the changes in soil chemical properties typically observed during old field succession. No important differences were detected between the plantations and the abandoned fields in terms of soil carbon accumulation, a result that was consistent across all sites. Previous research has shown that plantation establishment on former agricultural land tends to increase soil carbon stocks, but this varies greatly depending on previous land use, plantation type, and soil texture, among other factors (Laganière et al. 2010). Former plantations tend to accumulate less carbon when reforested than old cultivated fields, and since the majority of the abandoned fields in the present study were former pastures, this could have contributed to the lack of observed effect. In addition, the relatively low clay content of the soils under the plantations (see Table 2.1) could have slowed the formation of stable humus complexes (Laganière et al. 2010). Furthermore, ploughing as part of the site preparation for the plantations may have caused an initial decline in soil carbon (Laganière et al. 2010), followed by a gradual re-accumulation over the next ten years as the poplars grew. However, we did not observe any trend toward higher accumulation of carbon with faster poplar growth, suggesting that other factors may control the rate of carbon accumulation in the soil in these systems, or that any changes associated with ploughing or poplar growth were too small to detect. It must also be noted that because the primary objective of this study was to evaluate the understory habitat for plants, soil carbon was only measured between 5 cm and 10 cm, whereas a complete assessment of soil carbon dynamics would have required more detailed measurements of the entire soil profile.

The hybrid poplar plantations also failed to affect soil acidity and nutrient concentrations. It has been shown previously that during the natural afforestation of abandoned farmland in northeastern North America, soils tend to acidify and nitrogen tends to accumulate in the

system (Hooker and Compton 2003; Richter et al. 1994; Thorne and Hamburg 1985). However, in natural afforestation these changes take place over many decades. With an accelerated afforestation associated with hybrid poplar plantations, the soil acidity, C:N ratio and total N remained strongly correlated with stand age and uncorrelated with the stand basal area, suggesting that soil chemical properties may be necessarily slow to change, even if a tree canopy develops very quickly.

In contrast to soil properties, canopy development was significantly accelerated by the plantations compared to the unplanted portions of abandoned fields. Canopy development and the associated reduction in light availability are key changes associated with old field succession (Tilman 1985). A strong increase in leaf litter biomass also accompanied canopy development in the plantations and may also be an important factor for understory plants (Myster 1994). These environmental attributes were strongly related to basal area, regardless of the time that had passed since the abandonment of agriculture, indicating that their development can be accelerated by planting rapid-growing trees.

The development of a tree canopy in the plantations also reduced the humidity retained in the soil during a summer drought, compared to the adjacent fields. Because the plantations and the adjacent fields were assumed to have similar drainage characteristics, the reduction in soil moisture in the plantations is most likely explained by a higher transpiration rate of hybrid poplar trees, compared to the grasses and shrubs that occupied the abandoned fields. A similar result was found in a previous study comparing short-rotation plantations with cropland (Rijtema and De Vries 1994) An increase in water usage is also typical of increases in tree cover (Bosch and Hewlett 1982). On the other hand, the woodlots in this study retained on average more soil moisture than the plantations despite a higher average stand basal area. This could be explained by a higher transpiration rate of the fast-growing hybrid poplar trees than of the woodlot species. In a study in New England, early successional stands were found to have higher transpiration rates than mature stands despite a lower basal area (Hornbeck et al. 1997). The evapotranspiration rates of DxN hybrid poplar plantations were also found to be comparable to those of natural aspen stands in Minnesota (Perry et al. 2001). The lower soil moisture observed in the present study may therefore reflect different transpiration capacities of hybrid poplar stands vs. the mixed-species natural stands of the

woodlots, many of which were dominated by red maple (*Acer rubrum*) or white ash (*Fraxinus americana*). However, this difference in soil moisture could also be due to differences in drainage rather than evapotranspiration, reflecting the land-use history bias described above (poorly drained soils were abandoned the earliest).

2.4.2 Understory vegetation communities

The changes in abiotic and canopy characteristics of the plantations, as compared to the abandoned fields, prompted responses in the herb and shrub layer communities in terms of total cover and, to a lesser extent, composition. The total cover in the plantations was lower than in the fields, and intermediate in importance between the fields and the woodlots. This may be indicative of lower competition in the plantation understories than in the fields, creating a better chance for colonization and expansion by shade-tolerant species. In accordance with this hypothesis, we observed in the MxB poplar plantations a small but significant shift in the understory species composition toward that of the woodlots, compared to the abandoned fields (Fig 2.6). However, no such difference was observed in the DxN poplar plantations; rather, the understory vegetation in these plantations continued to resemble on average the unplanted fields.

Tree seedlings and saplings showed a greater response to the conditions created by the plantations, with significantly higher seedling-sapling abundances under both hybrid poplar clones, compared to the abandoned fields. The hybrid poplars therefore served as nurse plants, creating more favourable conditions for the establishment of seedlings. Several mechanisms have been suggested to account for the greater success of tree seedlings under nurse trees. First, the reduction in herbaceous plant cover can reduce competition for soil water (Burton and Bazzaz 1995; Davis et al. 1998), although this explanation is unlikely in the present study since hybrid poplar plantations actually reduced the soil water content compared to the adjacent fields. The reduction in herbaceous vegetation could also have reduced the competition for nitrogen (Burton and Bazzaz 1995), as well as allelopathy from certain species such as *Solidago* spp., which were abundant at many of the abandoned fields in this study (Horsley 1977). The reduction in light levels may have had a direct effect on

tree seedling growth by optimizing leaf carbon budgets (Laliberté et al. 2008). Finally, increases in leaf litter may have enhanced tree seedling emergence by modifying soil nitrogen (Pons 1989), soil moisture and temperature patterns (Barrett 1931; Burton and Bazzaz 1991), and/or reducing seed predation (Myster and Pickett 1993); however, the effects of leaf litter vary among tree species and litter type (Myster 1994).

Important differences were also observed among the study plots, with a considerably lower abundance of herbaceous plants and shrubs in plots with a high stand basal area, regardless of the type of environment. This relationship was likely due to differences in shading, leaf litter production, and other modifications of the environment associated with canopy development. In particular, the reduction in light levels under stands with larger basal areas may have eliminated or reduced the abundance of the most shade-intolerant species. However, other attributes of the plantations such as the increase in leaf litter abundance, the change in litter quality, the decreases in soil moisture, or other unmeasured changes associated with tree growth may also have contributed to the reduction in herb and shrub cover in the more productive plantations.

Canopy development and plantation productivity were also correlated with time since abandonment, which may be due to the hybrid poplars responding to the same soil and environmental characteristics that tended to influence abandonment; that is, the fields that were considered less suitable for agriculture or other uses and were abandoned earlier are also the fields that were less suitable for poplar growth (Truax et al., in preparation).

Fields that had been abandoned for longer before plantation establishment already had relatively well-developed populations of shrubs and tree seedlings and saplings, which were greatly disturbed by the site preparation for the hybrid poplar plantations, though a seed bank and vegetative propagules would have remained in the soil and the adjacent sections of undisturbed field may have served as dispersal sources for recolonization of the plantations. After ten years, the tree seedling and sapling populations had recovered to the level of the abandoned fields but the shrub covers in certain cases had not. A reduction in shrub cover in these plantations, compared to the neighbouring abandoned fields, may favour colonization by tree species, which can otherwise be impeded by dense covers of certain shrub species

such as *Cornus sericea* (Meilleur et al. 1994), which formed a very dense layer on several of the abandoned fields in this study. Nevertheless, the shrub abundance within these plantations remained higher than in the more productive plantations on recently abandoned fields. The overall understory species composition of the slower-growing plantations on long-abandoned fields tended to resemble the neighbouring fields in terms of overall species composition, showing neither a legacy of site preparation (except for the reduced shrub cover in some cases), nor an accelerated evolution of these communities toward that of a forest understory.

In contrast, on the more recently abandoned fields, the vegetation communities had had little time to develop before the establishment of the plantations and were dominated mainly by grasses. Therefore, the site preparation for the hybrid poplar plantations would have had little observable impact on the vegetation at these sites. These were also the sites at which the hybrid poplars grew exceptionally rapidly, and where the changes in light and litter conditions were the most dramatic. In these plantations the understory species composition had begun to shift in response to the change in environment, to resemble slightly more the vegetation communities of the woodlots, and they tended to favour the establishment of shrubs and tree seedlings compared to the unplanted fields. The changes in species composition may reflect a shift in dominance from shade-intolerant to more shade-tolerant species, and a reduction in the dominance of grasses to make space for shrubs and understory herb species. The cover of introduced species, on the other hand, did not appear to vary in relation to the growth rate of the hybrid poplar trees or the age of the abandoned fields. The abundance of many of the introduced species in this study may, therefore, depend more on soil or biotic variables than on canopy development.

Regardless of the growth rate of the hybrid poplar trees or the age of the pre-existing abandoned field, the understory species composition in the plantations remained very different from that of the woodlots after ten years, and generally contained a lower seedling and sapling abundance and a higher introduced species cover. Differences in species composition among the plots were most strongly correlated with the age of the stand rather than the stand basal area or any environmental characteristic (Fig. 2.5). This result suggests a dispersal limitation, with the chance of dispersal increasing with longer times since the

abandonment of agriculture, or since the last major disturbance (Flinn and Vellend 2005). Further research is needed to test this hypothesis, which could include an assessment of the correlation between the proximity of seed sources in the landscape and species composition in the plantations. Informal observations in this study support such a trend, with the St-Adrien plantation, which was located just beside a woodlot, having a much higher abundance of tree seedlings than plantations that were not as close to a tree seed source (K. Boothroyd-Roberts, field observations and Fig. 2.2). Although many early successional tree species in northeastern North America are wind-dispersed, and are therefore less limited by dispersal than many understory herb species, the stand basal area explained only 27% of the variability in seedling and sapling abundance among the study plots, indicating that other factors, such as the landscape context, may have played an important role in determining the rate of colonization of the plantations by tree seedlings and saplings.

As an alternative hypothesis, the large differences observed between the woodlot and plantation understory vegetation communities could also have been due to environmental differences that prevented the colonization of the plantations by certain forest understory species or limited their competitive ability (Honnay et al. 1999). For example, soil properties, moisture availability, or leaf litter composition were different in the plantations from any of the woodlots and may have been unsuitable for certain forest species.

2.4.3 Clone effects

At all but the lowest elevation, the MxB poplar plantations were somewhat more productive and showed better survival, while at the Bedford site the trend was reversed (Truax et al., in preparation). The two clones also differed in growth form, with the MxB poplars producing a denser network of roots near the surface along with numerous root suckers (K. Boothroyd-Roberts, field observations). The results of the present study also show that the MxB clone was associated with a greater degree of canopy closure, denser shade, and more abundant leaf litter produced in the MxB poplar plantations. This could be explained by a greater allocation of biomass to leaves and branches in the MxB clone than the DxN clone (Fortier et al. 2010a). The differences in environmental attributes created by the two clones produced

differences in the understory vegetation communities, particularly in the cover of the herb and shrub layers, which was considerably lower under the MxB poplars compared to under the DxN poplars. This difference appears to extend beyond simply the differences in light availability or litter abundance. A similar reduction in understory vegetation biomass was observed by Fortier and colleagues under a different MxB poplar clone (Fortier et al. 2011). One possible explanation for such a difference is the effects of secondary chemicals in the leaves of the MxB clone. Previous studies have shown that secondary chemicals in the leaves of *Populus balsamifera*, one of the parent species of the MxB clone in this study, can reduce nitrogen availability in the soil, thus having a negative effect on competing species (Schimel et al. 1998). Furthermore, the greater observed root density of the MxB clone may allow it to compete more efficiently for scarce available nitrogen than species with lower root densities (Fischer et al. 2006). The understory species composition had shifted slightly closer to that of a woodlot under the more productive MxB poplar plantations than under the productive DxN plantations; however, the MxB poplar plantations also contained more introduced species in their understories. More research is needed, therefore, to assess which of the two clones is more efficient for encouraging the development of a forest-like understory environment and vegetation community.

2.5 Conclusions

The general patterns observed across the study sites suggest that hybrid poplar plantations have the potential to both accelerate and interfere with the development of a forest-like understory environment, when compared to the alternative of allowing the field to follow a course of old field succession to a forest. One potential source of interference is in the site preparation phase, which represents a major disturbance, effectively resetting succession to an earlier stage. This effect could be more important on sites that have been abandoned for longer and have already begun to be colonized by tree species and mid-successional species. Other phases of the plantation cycle may also be associated with disturbances resulting from periodic vegetation control, pruning, thinning, and harvesting (Archaux et al. 2010). In addition, a hybrid poplar plantation may interfere with the development of an understory vegetation community by creating an environment with attributes outside of the normal range

found in natural environments. For example, it is not clear what the implications may be for understory plants of a potentially high evapotranspiration rate, or the effects on nutrient cycling of the litter quality of poplar leaves (especially leaves from a hybrid poplar of *P. balsamifera* parentage) compared to litter from a more diverse canopy.

On the other hand, a hybrid poplar need not be seen as an endpoint, but rather as a transitional stage between an open field environment and some other type of stand. The results of this study suggest that hybrid poplar plantations can accelerate the transition to a natural forest stand by facilitating the colonization of a site by tree species. This role has already been described for plantations on degraded tropical fields (Carnevale and Montagnini 2002) and for clumps of trees or shrubs in temperate region old fields (Li and Wilson 1998). One mechanism for this effect may be the suppression of shade-intolerant, competitive species, which could otherwise prevent the growth of tree seedlings. Previous studies have suggested that the development of a dense shrub layer on abandoned fields can delay succession by preventing the growth of tree seedlings (Meilleur et al. 1994), while site preparation for a plantation would remove this limiting factor. Plantations can also suppress the open field species such as open field grasses through the shade created by their canopies. The suppression of certain competitive species could also allow for under-planting with shade-tolerant tree species or intentional introductions of understory plant species. However, further research is required to directly test the quality of the hybrid poplar plantation habitat for understory vegetation (e.g., through transplantation experiments), independently of dispersal limitations.

The net effect of a hybrid poplar plantation on the understory vegetation community appears to be more favourable to the acceleration of succession on recently-abandoned fields and where the planted trees grow quickly. Our results suggest that on a long-abandoned field with poor soils, the herb and shrub communities may take more than a decade to recover from the disturbances of site preparation, although these plantations could still potentially accelerate succession over the long term if the hybrid poplar trees develop a closed canopy more quickly than the trees that naturally colonize the fields (which appeared likely in the sites in this study). However, on recently-abandoned, productive sites, hybrid poplar plantations appear to be a promising avenue for active afforestation.

2.6 References

Archaux, F., R. Chevalier and A. Berthelot. 2010. Towards practices favourable to plant diversity in hybrid poplar plantations. Forest Ecology and Management **259**(12): 2410-2417.

Aubin, I., C. Messier and A. Bouchard. 2008. Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biological Conservation **141**(10): 2461-2476.

Barrett, L.I. 1931. Influence of forest litter on the germination and early survival of chestnut oak, *Quercus montana*, Willd. Ecology **12**(3): 476-484.

Bélanger, L. and M. Grenier. 2002. Agriculture intensification and forest fragmentation in the St. Lawrence Valley, Québec, Canada. Landscape Ecology **17**(6): 495-507.

Benjamin, K., G. Domon and A. Bouchard. 2005. Vegetation composition and succession of abandoned farmland: Effects of ecological, historical and spatial factors. Landscape Ecology **20**: 627-647.

Bobiec, A. 1998. The mosaic diversity of field layer vegetation in the natural and exploited forests of Bialowieza. Plant Ecology **136**(2): 175-187.

Bosch, J.M. and J.D. Hewlett. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. Journal of Hydrology **55**(1-4): 3-23.

Brouillet, L., F. Coursol, M. Favreau and M. Anions. 2010. VASCAN, the Database of Vascular Plants of Canada.

Brunet, J. and G. Von Oheimb. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology **86**(3): 429-438.

Burton, P.J. and F.A. Bazzaz. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. American Journal of Botany **78**(1): 131-149.

Burton, P.J. and F.A. Bazzaz. 1995. Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. Journal of Ecology **83**(1): 99-112.

Carnevale, N.J. and F. Montagnini. 2002. Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. Forest Ecology and Management **163**(1-3): 217-227.

Chazdon, R.L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science **320**(5882): 1458-1460.

D'Orangeville, L., A. Bouchard and A. Cogliastro. 2008. Post-agricultural forests: Landscape patterns add to stand-scale factors in causing insufficient hardwood regeneration. Forest Ecology and Management **255**(5-6): 1637-1646.

Davis, M.A., K.J. Wrage and P.B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology **86**(4): 652-661.

De Keersmaeker, L., L. Martens, K. Verheyen, M. Hermy, A. De Schrijver and N. Lust. 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). Forest Ecology and Management **188**(1-3): 291-304.

Dölle, M. and W. Schmidt. 2009. Impact of tree species on nutrient and light availability: Evidence from a permanent plot study of old-field succession. Plant Ecology **203**(2): 273-287.

Domon, G. and A. Bouchard. 2007. The landscape history of Godmanchester (Quebec, Canada): Two centuries of shifting relationships between anthropic and biophysical factors. Landscape Ecology **22**(8): 1201-1214.

Fischer, D., S. Hart, B. Rehill, R. Lindroth, P. Keim and T. Whitham. 2006. Do high-tannin leaves require more roots? Oecologia **149**(4): 668-675.

Flinn, K.M. and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment **3**(5): 243-250.

Fortier, J., D. Gagnon, B. Truax and F. Lambert. 2010a. Biomass and volume yield after 6 years in multiclonal hybrid poplar riparian buffer strips. Biomass and Bioenergy **34**(7): 1028-1040.

Fortier, J., D. Gagnon, B. Truax and F. Lambert. 2010b. Nutrient accumulation and carbon sequestration in 6-year-old hybrid poplars in multiclonal agricultural riparian buffer strips. Agriculture, Ecosystems & Environment **137**(3-4): 276-287.

Fortier, J., D. Gagnon, B. Truax and F. Lambert. 2011. Understory plant diversity and biomass in hybrid poplar riparian buffer strips in pastures. New Forests (in press).

Foster, D.R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology **80**(4): 753-771.

Gachet, S., A. Leduc, Y. Bergeron, T. Nguyen-Xuan and F. Tremblay. 2007. Understory vegetation of boreal tree plantations: Differences in relation to previous land use and natural forests. Forest Ecology and Management **242**(1): 49-57.

Glitzenstein, J.S., C.D. Canham, M.J. McDonnell and D.R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bulletin of the Torrey Botanical Club **117**(2): 106-122.

Honnay, O., M. Hermy and P. Coppin. 1999. Impact of habitat quality on forest plant species colonization. Forest Ecology and Management **115**(2-3): 157-170.

Honnay, O., K. Verheyen, J. Butaye, H. Jacquemyn, B. Bossuyt and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters **5**(4): 525-530.

Hooker, T.D. and J.E. Compton. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecological Applications **13**(2): 299-313.

Hornbeck, J.W., C.W. Martin and C. Eagar. 1997. Summary of water yield experiments at Hubbard Brook Experimental Forest, New Hampshire. Canadian Journal of Forest Research **27**(12): 2043-2052.

Horsley, S.B. 1977. Allelopathic inhibition of black cherry by fern, grass, goldenrod, and aster. Canadian Journal of Forest Research **7**: 205-216.

Jeffries, S.B., T.R. Wentworth and H.L. Allen. 2010. Long-term effects of establishment practices on plant communities across successive rotations in a loblolly pine (*Pinus taeda*) plantation. Forest Ecology and Management **260**(9): 1548-1556.

Laganière, J., D.A. Angers and D. Paré. 2010. Carbon accumulation in agricultural soils after afforestation: A meta-analysis. Global Change Biology **16**(1): 439-453.

Laliberté, E., A. Bouchard and A. Cogliastro. 2008. Optimizing hardwood reforestation in old fields: The effects of treeshelters and environmental factors on tree seedling growth and physiology. Restoration Ecology **16**(2): 270-280.

Le Houérou, H.N. 1993. Land degradation in Mediterranean Europe: Can agroforestry be a part of the solution? A prospective review. Agroforestry Systems **21**(1): 43-61.

Li, X. and S.D. Wilson. 1998. Facilitation among woody plants establishing in an old field. Ecology **79**(8): 2694-2705.

Meilleur, A., H. Véronneau and A. Bouchard. 1994. Shrub communities as inhibitors of plant succession in southern Quebec. Environmental Management **18**(6): 907-921.

Myster, R.W. 1994. Contrasting litter effects on old field tree germination and emergence. Plant Ecology **114**(2): 169-174.

Myster, R.W. and S.T.A. Pickett. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos **66**(3): 381-388.

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens and H. Wagner. 2010. Vegan: community ecology package, version 1.17-4. R project for statistical computing.

Paquette, A. and C. Messier. 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment **8**(1): 27-34.

Perry, C.H., R.C. Miller and K.N. Brooks. 2001. Impacts of short-rotation hybrid poplar plantations on regional water yield. Forest Ecology and Management **143**(1-3): 143-151.

Peterken, G.F. 2000. Rebuilding networks of forest habitats in lowland England. Landscape Research **25**(3): 291-303.

Pickett, S.T.A. 1982. Population patterns through twenty years of oldfield succession. Vegetatio **49**(1): 45-59.

Pons, T.L. 1989. Breaking of seed dormancy by nitrate as a gap detection mechanism. Annals of Botany **63**(1): 139-143.

Poulton, P.R., E. Pye, P.R. Hargreaves and D.S. Jenkinson. 2003. Accumulation of carbon and nitrogen by old arable land reverting to woodland. Global Change Biology **9**(6): 942-955.

Poyatos, R., J. Latron and P. Llorens. 2003. Land use and land cover change after agricultural abandonment: The case of a Mediterranean Mountain area (Catalan Pre-Pyrenees). Mountain Research and Development **23**(4): 362-368.

Richter, D.D., D. Markewitz, C.G. Wells, H.L. Allen, R. April, P.R. Heine and B. Urrego. 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. Ecology **75**(5): 1463-1473.

Rijtema, P.E. and W. De Vries. 1994. Differences in precipitation excess and nitrogen leaching from agricultural lands and forest plantations. Biomass and Bioenergy **6**(1-2): 103-113.

Robertson, G.P. and P.M. Vitousek. 1981. Nitrification potentials in primary and secondary succession. Ecology **62**(2): 376-386.

Roura-Pascual, N., P. Pons, M. Etienne and B. Lambert. 2005. Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. Mountain Research and Development **25**(3): 252-261.

Schimel, J.P., R.G. Cates and R. Ruess. 1998. The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan Taiga. Biogeochemistry **42**(1): 221-234.

Shannon, C.E. and W. Weaver. 1949. The Mathematical Theory of Communication. Urbana, IL, University of Illinois Press.

Singleton, R., S. Gardescu, P.L. Marks and M.A. Geber. 2001. Forest herb colonization of postagricultural forests in central New York State, USA. Journal of Ecology **89**(3): 325-338.

Soo, T., A. Tullus, H. Tullus and E. Roosaluste. 2009. Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments. Forest Ecology and Management **257**(3): 858-867.

Stephens, S.S. and M.R. Wagner. 2007. Forest plantations and biodiversity: A fresh perspective. Journal of Forestry **105**(6): 307-313.

Stevens, A. and B. van Wesemael. 2008. Soil organic carbon stock in the Belgian Ardennes as affected by afforestation and deforestation from 1868 to 2005. Forest Ecology and Management **256**(8): 1527-1539.

Thorne, J.F. and S.P. Hamburg. 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. Ecology **66**(4): 1333-1338.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. The American Naturalist **125**(6): 827-852.

Truax, B. and D. Gagnon. 2008. Mesurage après 8 ans et élaboration d'équations prédictives de rendement de peuplier hybrides plantés en friches d'origine agricole en Estrie. Rapport final, Table des MRC de l'Estrie, Programme Volet II (projet E07-51), 19pp.

Truax, B., D. Gagnon, J. Fortier and F. Lambert. Biomass and volume yield after 8 years in multi-clonal hybrid poplar plantations on abandoned agricultural land along a climatic gradient in southern Quebec, Canada (in preparation).

Truax, B., F. Lambert and D. Gagnon. 2000. Herbicide-free plantations of oaks and ashes along a gradient of open to forested mesic environments. Forest Ecology and Management. **137**: 155-169.

USDA, NRCS. 2011. The PLANTS Database. National Plant Data Center, Baton Rouge, LA 70874-4490 USA. Retrieved April 24, 2011, from http://plants.usda.gov.

Table 2.1 Characteristics of the eight hybrid poplar plantation study sites in the Eastern Townships region of Quebec, Canada

					Woodlot	Field and plantation				
Plantation sites (abbreviations)	Elevation (m)	Temperature: Mean annual (°C)	Degree days (>5°C)	Precipitation: Mean annual (mm)	Minimum stand age (years)	Estimated age since abandonment (years)	Clay ($g\ kg^{-1}$)	Silt ($g\ kg^{-1}$)	Sand ($g\ kg^{-1}$)	Textural class
Bedford (BED)	80	6.0	2061.3	1156.2	29 - 54	≤ 15	183	267	550	Sandy loam
Bromptonville (BRO)	170	5.3	1884.1	1149.8	34	≤ 15	287	517	197	Clay Loam
Ste-Catherine (CAT)	230	5.3	1859.9	1134.5	21 - 42	20 - 30	123	453	423	Loam
Ogden (OGD)	260	5.1	1805.6	1155.6	39	20 - 30	130	480	390	Loam
St-Adrien (ADR)	320	4.0	1648.5	1198.7	38	20 - 30	117	450	433	Loam
Melbourne (MEL)	330	5.3	1860.7	1110.5	28 – 31	20 - 30	137	447	416	Loam
La Patrie (LAP)	440	3.7	1582.8	1297.5	58	≤ 15	123	553	323	Silty loam
Stornoway (STO)	450	3.3	1489.9	1322.4	23	30 - 40	100	483	417	Silty loam

Table 2.2 Results from ANOVAs (F and p-values) on environmental and vegetation attributes of experimental plantations of two hybrid poplar clones, abandoned fields, and woodlots at 8 study sites in the Eastern Townships region of Quebec, Canada

	Environment		Site		Environment * Site	
Variable	F	p-value	F	p-value	F	p-value
Soil chemical properties						
pH	13.06	<0.001	13.87	<0.001	6.68	<0.001
C	19.76	<0.001	13.34	<0.001	1.87	0.030
N	5.93	0.001	10.22	<0.001	1.87	0.029
C:N ratio	38.84	<0.001	23.34	<0.001	2.35	0.005
P	1.11	0.352	13.52	<0.001	2.07	0.014
Ca	0.11	0.954	21.45	<0.001	8.03	<0.001
K	10.08	<0.001	7.92	<0.001	2.42	0.004
Mg	9.04	<0.001	9.77	<0.001	5.50	<0.001
Soil humidity						
June	8.16	<0.001	13.10	<0.001	1.65	0.064
August	9.33	<0.001	8.84	<0.001	3.05	<0.001
Canopy and litter						
Stand basal area of trees	500.91	<0.001	18.87	<0.001	6.18	<0.001
Canopy openness	313.39	<0.001	22.14	<0.001	4.84	<0.001
Light transmitted through canopy	256.34	<0.001	28.00	<0.001	4.73	<0.001
Leaf litter biomass	191.00	<0.001	12.67	<0.001	4.70	<0.001
Understory vegetation						
Seedling-sapling abundance index	102.44	<0.001	29.86	<0.001	3.22	<0.001
Fraxinus spp. seedling abundance index	23.04	<0.001	24.21	<0.001	2.52	0.002
Acer rubrum seedling abundance index	28.81	<0.001	5.68	<0.001	7.78	<0.001
Betula spp. seedling abundance index	0.50	0.681	18.05	<0.001	2.38	0.004
Herb and shrub diversity (Shannon)	5.11	0.003	2.97	0.009	2.09	0.013
Total cover of herb/shrub layer	75.00	<0.001	14.72	<0.001	7.51	<0.001
Total cover of shrubs	4.47	0.007	39.90	<0.001	2.85	0.001
Relative cover of introduced species	27.69	<0.001	12.25	<0.001	1.87	0.029

Note: Results are from two-way fixed-factor ANOVAs using 12 m x 12 m (soil, substrate, and canopy variables) or 8 m x 7 m (understory vegetation) plots as the experimental units. Degrees of freedom were as follows: Environment: 3, Site: 7, Environment*Site: 21, Residual: 64.

Table 2.3 Characteristics of experimental plantations of two hybrid poplar clones and of two adjacent natural environments (means ± standard error and p-values of ANOVAs) across 8 study sites in the Eastern Townships region of Quebec, Canada[1]

		Plantation		Natural regeneration		
Variable	Units	*Populus maximowiczii* x *P. balsamifera*	*P. deltoides* x *P. nigra*	Abandoned field	Woodlot	p-value for environment effect
Soil chemical properties[2]						
pH		4.87 ± 0.08 (a)	4.91 ± 0.08 (a)	4.94 ± 0.06 (a)	4.48 ± 0.17 (b)	<0.001
C	mg/g	34.4 ± 2.2 (b)	32.9 ± 2.1 (b)	34.7 ± 1.7 (b)	49.5 ± 3.3 (a)	<0.001
N	mg/g	3.25 ± 0.14 (b)	3.18 ± 0.14 (b)	3.30 ± 0.11 (b)	3.97 ± 0.24 (a)	0.001
C:N ratio		10.39 ± 0.28 (b)	10.18 ± 0.29 (b)	10.43 ± 0.28 (b)	12.41 ± 0.22 (a)	<0.001
P	µg/g	28.5 ± 4.1	24.3 ± 2.3	25.6 ± 2.1	20.8 ± 1.8	0.352
Ca	µg/g	815 ± 92	797 ± 82	814 ± 86	973 ± 208	0.954
K	µg/g	36.2 ± 3.5 (b)	29.7 ± 1.7 (b)	35.4 ± 3.0 (b)	46.1 ± 3.2 (a)	<0.001
Mg	µg/g	45.4 ± 5.5 (b)	50.5 ± 5.1 (b)	56.1 ± 6.9 (b)	87.6 ± 11.6 (a)	<0.001
Soil humidity						
June	g/g	0.37 ± 0.03 (b)	0.37 ± 0.02 (b)	0.42 ± 0.02 (ab)	0.48 ± 0.03 (a)	<0.001
August	g/g	0.36 ± 0.02 (b)	0.37 ± 0.02 (b)	0.47 ± 0.04 (a)	0.49 ± 0.03 (a)	<0.001
Canopy and litter						
Stand basal area of trees	m^2/ha	16.0 ± 1.6 (b)	15.0 ± 2.3 (b)	0.4 ± 0.2 (c)	28.2 ± 2.9 (a)	<0.001
Canopy openness	%	18.8 ± 1.8 (c)	21.9 ± 2.0 (b)	54.5 ± 3.0 (a)	12.1 ± 0.5 (d)	<0.001
Light transmitted through canopy	mol/m^2/day	8.39 ± 1.09 (c)	10.09 ± 1.22 (b)	26.37 ± 1.52 (a)	5.82 ± 0.29 (d)	<0.001
Leaf litter biomass	g/m^2	422 ± 40 (a)	326 ± 33 (b)	52 ± 12 (c)	479 ± 28 (a)	<0.001

Table 2.3 continued

Variable	Units	Plantation		Natural regeneration		p-value for environment effect
		Populus maximowiczii x *P. balsamifera*	*P. deltoides* x *P. nigra*	Abandoned field	Second-growth woodlot	
Understory vegetation						
Seedling-sapling abundance index	/ha index[3]	1006 ± 468 (b)	1058 ± 527 (b)	587 ± 275 (c)	4278 ± 579 (a)	<0.001
Fraxinus spp. seedling abundance index	/ha index[3]	224 ± 137 (b)	162 ± 111 (bc)	76 ± 46 (c)	2006 ± 608 (a)	<0.001
Acer rubrum seedling abundance index	/ha index[3]	23 ± 13 (b)	21 ± 9 (b)	20 ± 11 (b)	518 ± 230 (a)	<0.001
Betula spp. seedling abundance index	/ha index[3]	708 ± 445	828 ± 499	377 ± 216	192 ± 70	0.681
Herb and shrub diversity (Shannon)		2.15 ± 0.05 (ab)	2.01 ± 0.06 (b)	2.08 ± 0.04 (b)	2.33 ± 0.09 (a)	0.003
Total cover of herb/shrub layer	%	163 ± 19 (c)	203 ± 13 (b)	256 ± 18 (a)	93 ± 8 (d)	<0.001
Total cover of shrubs	%	14 ± 3 (b)	20 ± 5 (ab)	28 ± 8 (b)	23 ± 6 (a)	0.007
Relative cover of introduced species	%	47 ± 5 (a)	40 ± 5 (a)	46 ± 5 (a)	15 ± 4 (b)	<0.001

[1]For each variable, values followed by the same letter did not differ significantly in Tukey HSD means comparisons test (alpha = 0.05). p-values are from two-way ANOVAs on environment (4 levels) and site (8 levels), with 3 replicates per cell.
[2]All soil properties were measured between 5 cm and 10 cm depth.
[3]Seedling-sapling abundance index calculated as: number of saplings / ha + (0.1 * number of seedlings / ha)

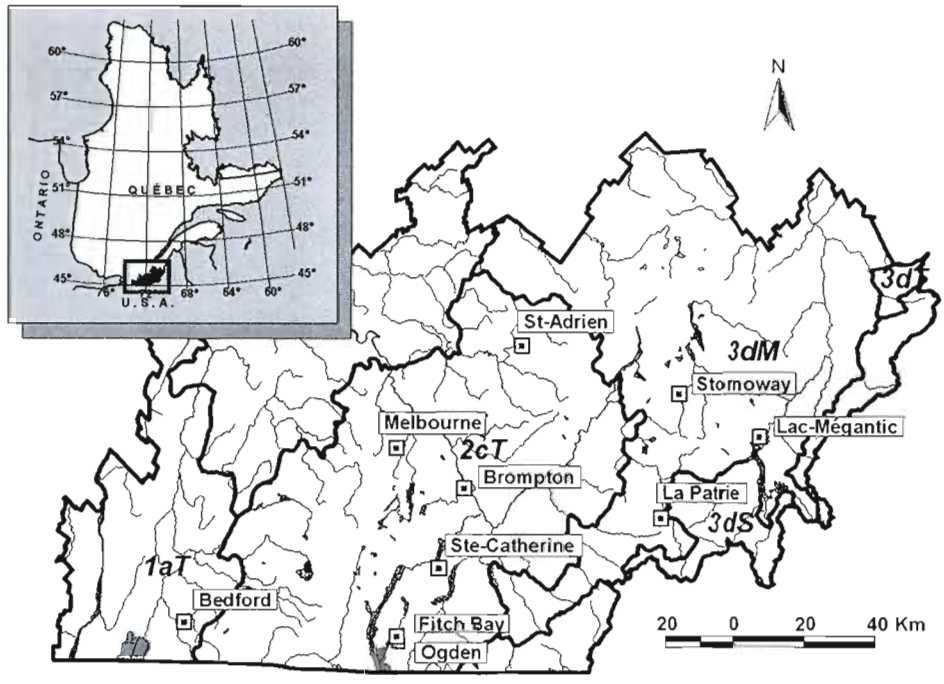

Figure 2.1 Study sites in the Eastern Townships region of Quebec, Canada. Ecological zones are also indicated (see text for details). The Fitch Bay and Lac-Mégantic sites were excluded from this study.

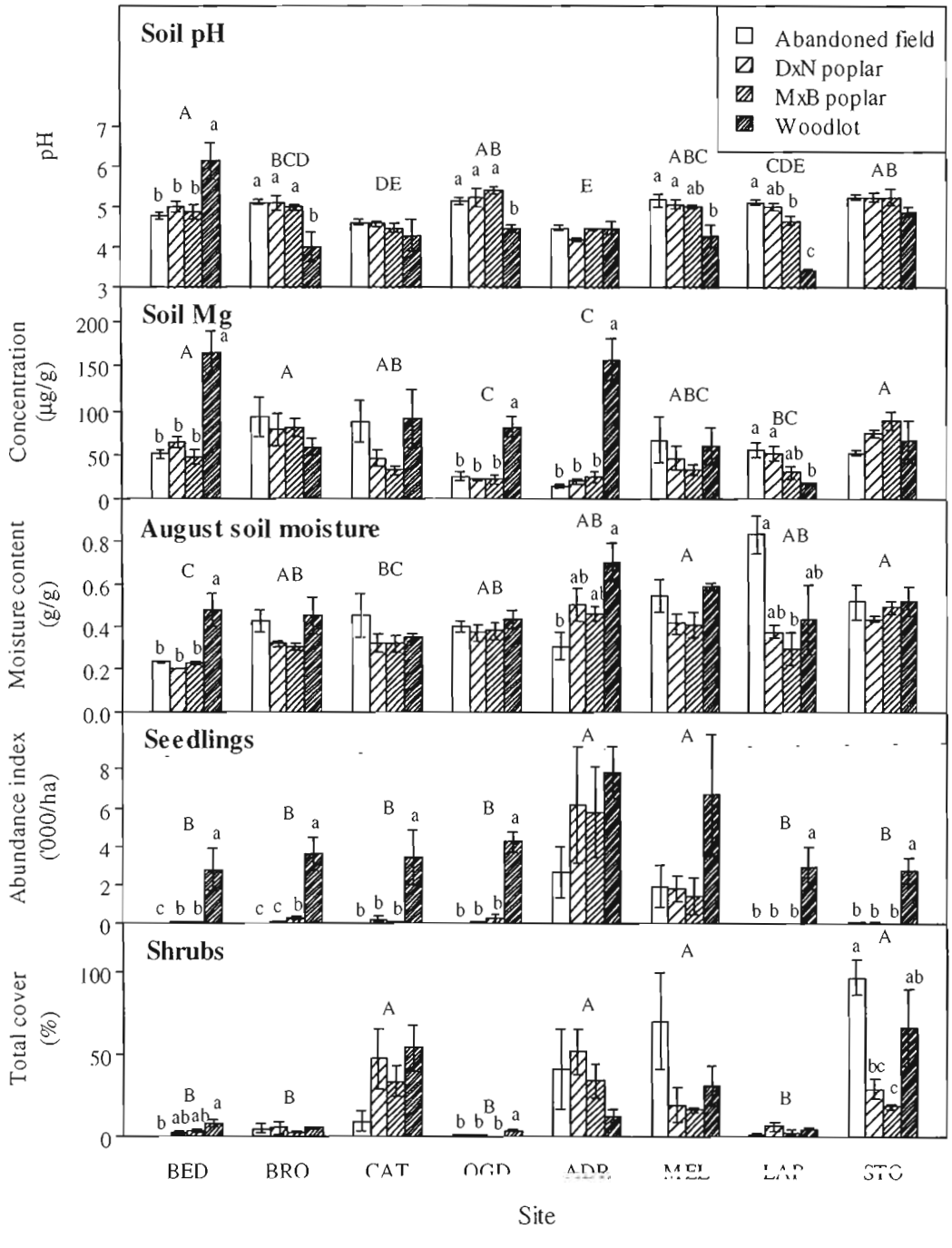

Figure 2.2 Selected attributes of plantations of two hybrid poplar clones, abandoned fields and natural woodlots at 8 sites, ordered from lowest to highest elevation (means and s.e.). Different uppercase letters indicate significant overall differences between sites and lowercase letters indicate differences between environments within a site ($p < 0.05$).

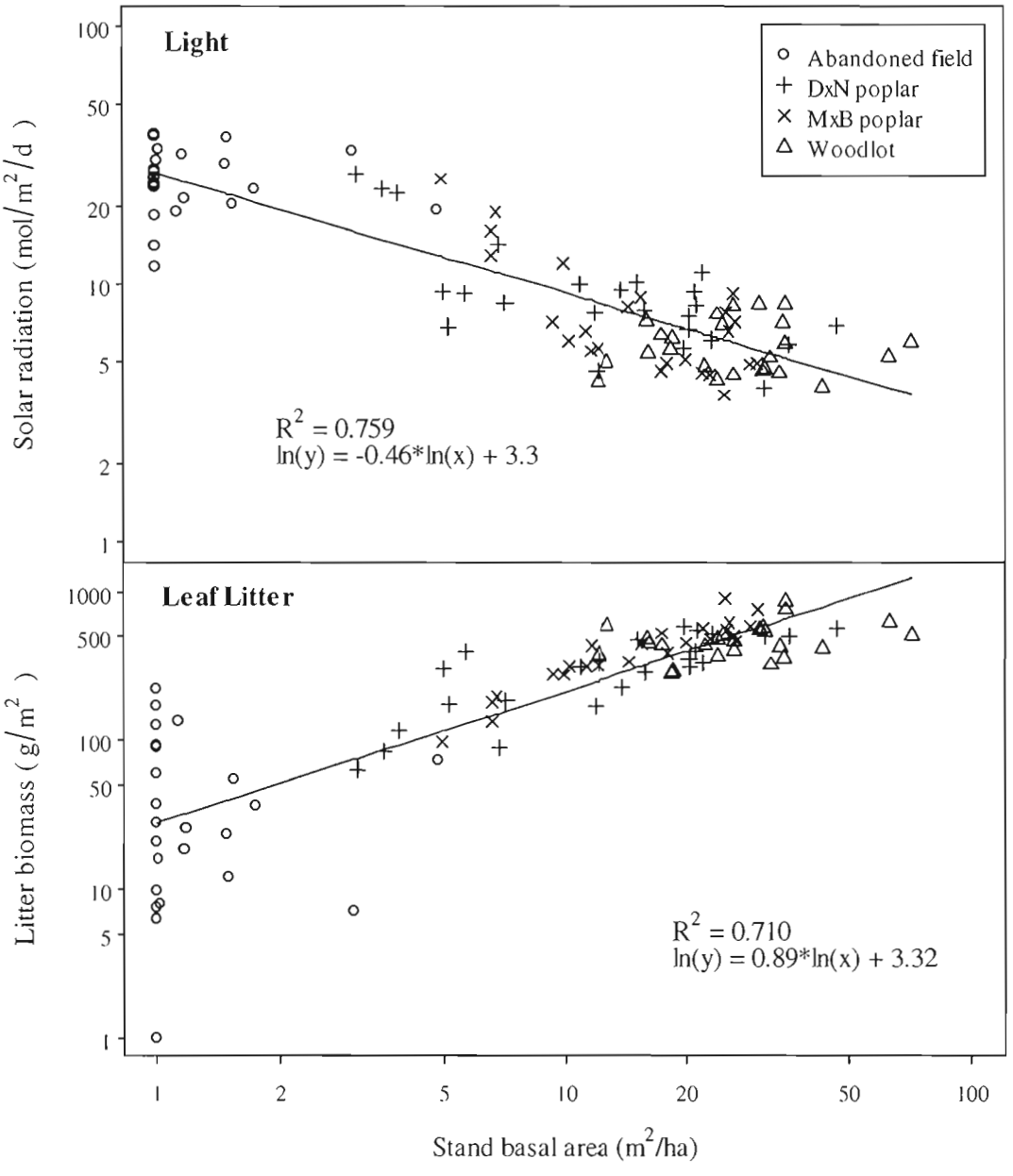

Figure 2.3 Solar radiation transmitted through the canopy and leaf litter biomass in late fall in relation to stand basal area in plantations of two hybrid poplar clones, abandoned fields and natural woodlots. DxN poplar and MxB poplar: plantations of a DxN and an MxB hybrid poplar clone; Woodlot: second-growth hardwood woodlot. One unit was added to all basal area and leaf litter data points to allow plotting 0-values on a log scale. Regression lines were fit to the combined data from the four environments.

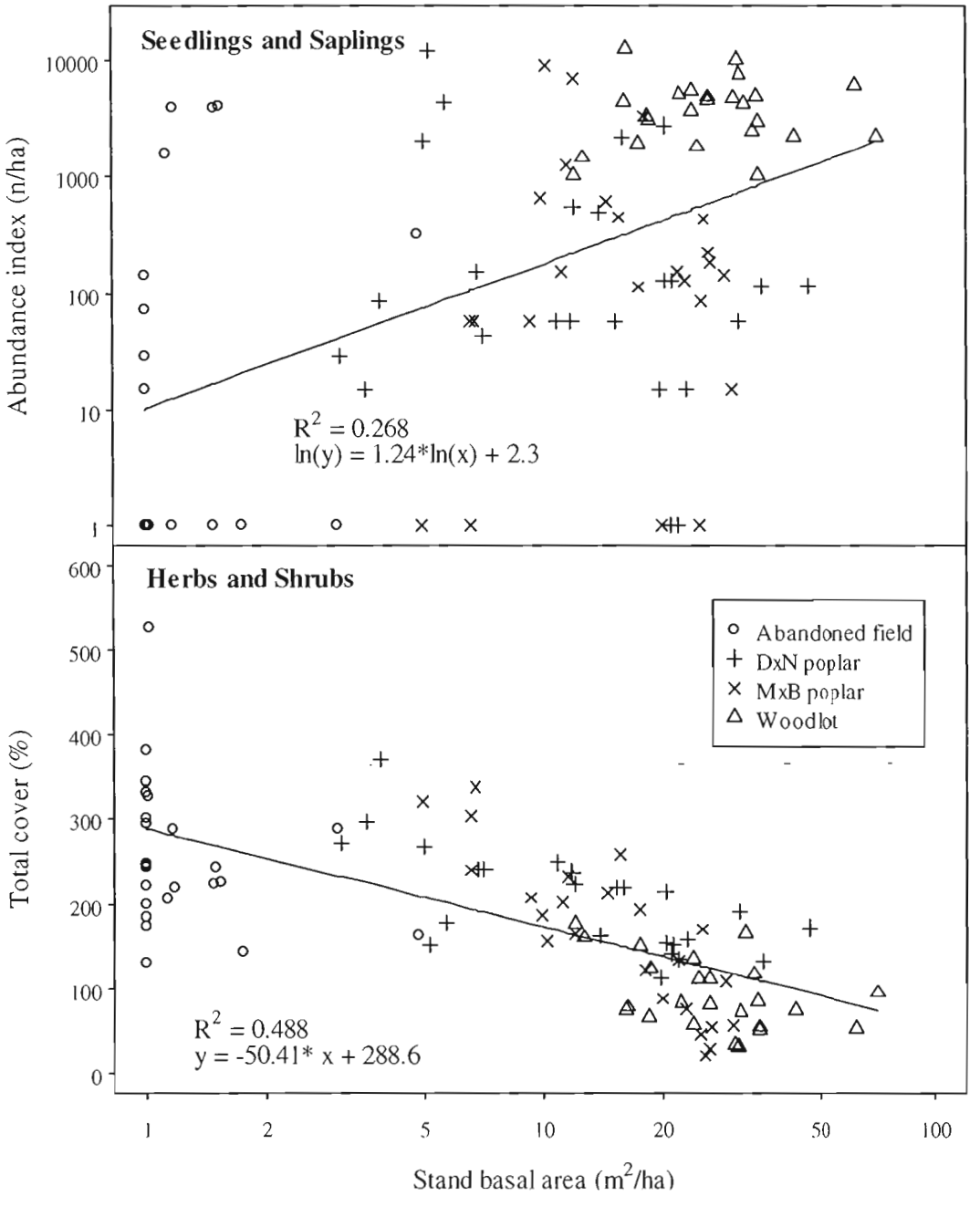

Figure 2.4 Tree seedling-sapling abundance index (see text for details) and total herb and shrub cover in relation to stand basal area in plantations of two hybrid poplar clones, abandoned fields and natural woodlots. DxN poplar and MxB poplar: plantations of a DxN and an MxB hybrid poplar clone; Woodlot: second-growth hardwood woodlot. One unit was added to all basal area and seedling data points to allow plotting 0-values on a log scale. The seedling-sapling regression line was fit to the combined data from the four environments.

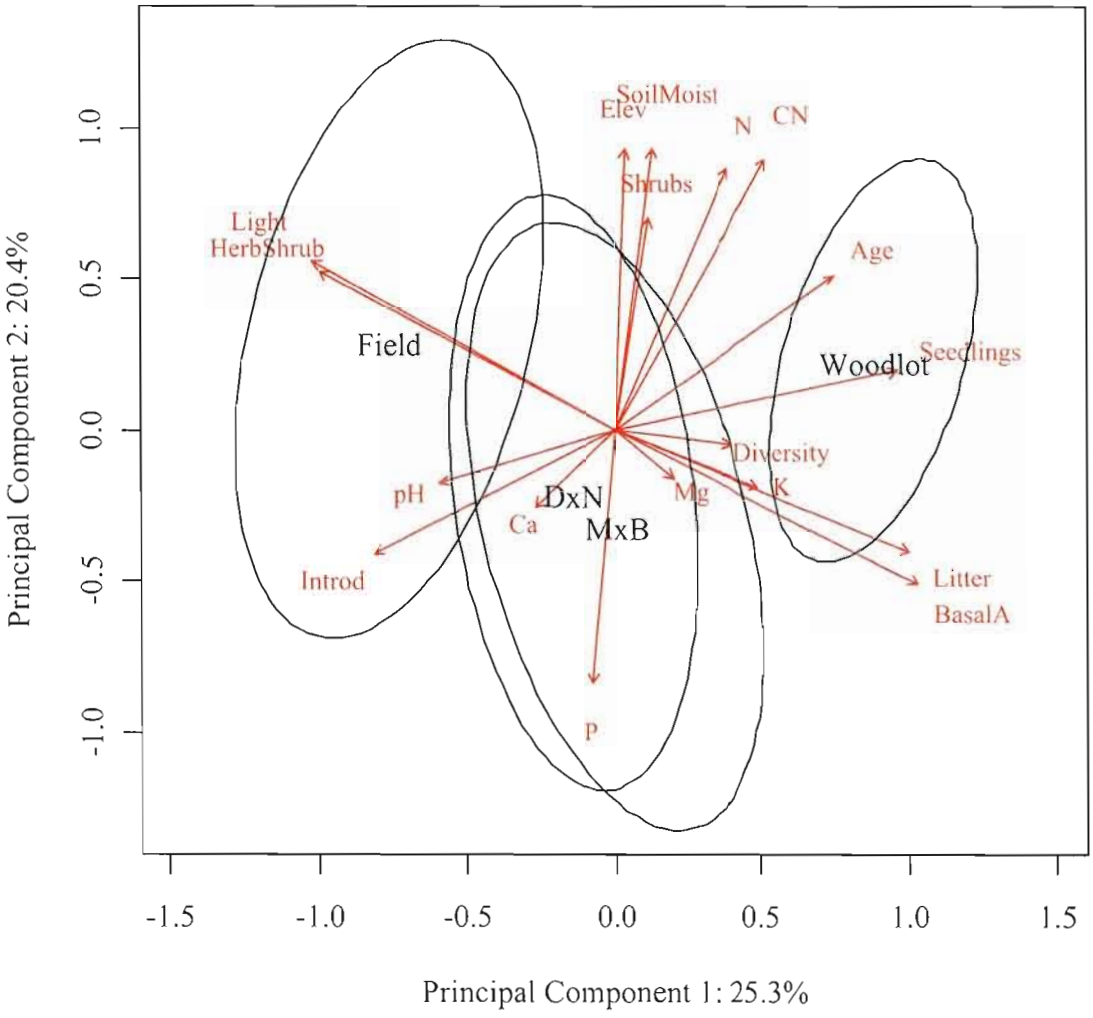

Figure 2.5 First two axes of a Principal Component Analysis of abiotic and biotic attributes of plantations of two hybrid poplar clones, abandoned fields and natural woodlots at each of eight sites distributed along an elevation gradient. In black, 68% confidence ellipses of plots within the four environments with labels representing the centroids (Field: abandoned field, DxN poplar: plantation of a DxN poplar clone; MxB poplar: plantation of an MxB poplar clone; Woodlot: second-growth hardwood woodlot). In red, environmental attributes (Elev: site elevation; P, K, Mg, Ca and N: soil nutrient concentrations; pH: soil pH; CN: soil C:N ratio; SoilMoist: soil moisture in August; Litter: leaf litter biomass in late fall, Age: time since last disturbance; BasalA: stand basal area; Light: solar radiation transmitted through the canopy; Seedlings: tree seedling-sapling abundance index (see text for details); Shrubs: total cover of shrubs; HerbShrub: percent cover of herb/shrub layer vegetation; Diversity: Shannon's diversity index of herb/shrub vegetation; Introd: relative abundance of introduced species).

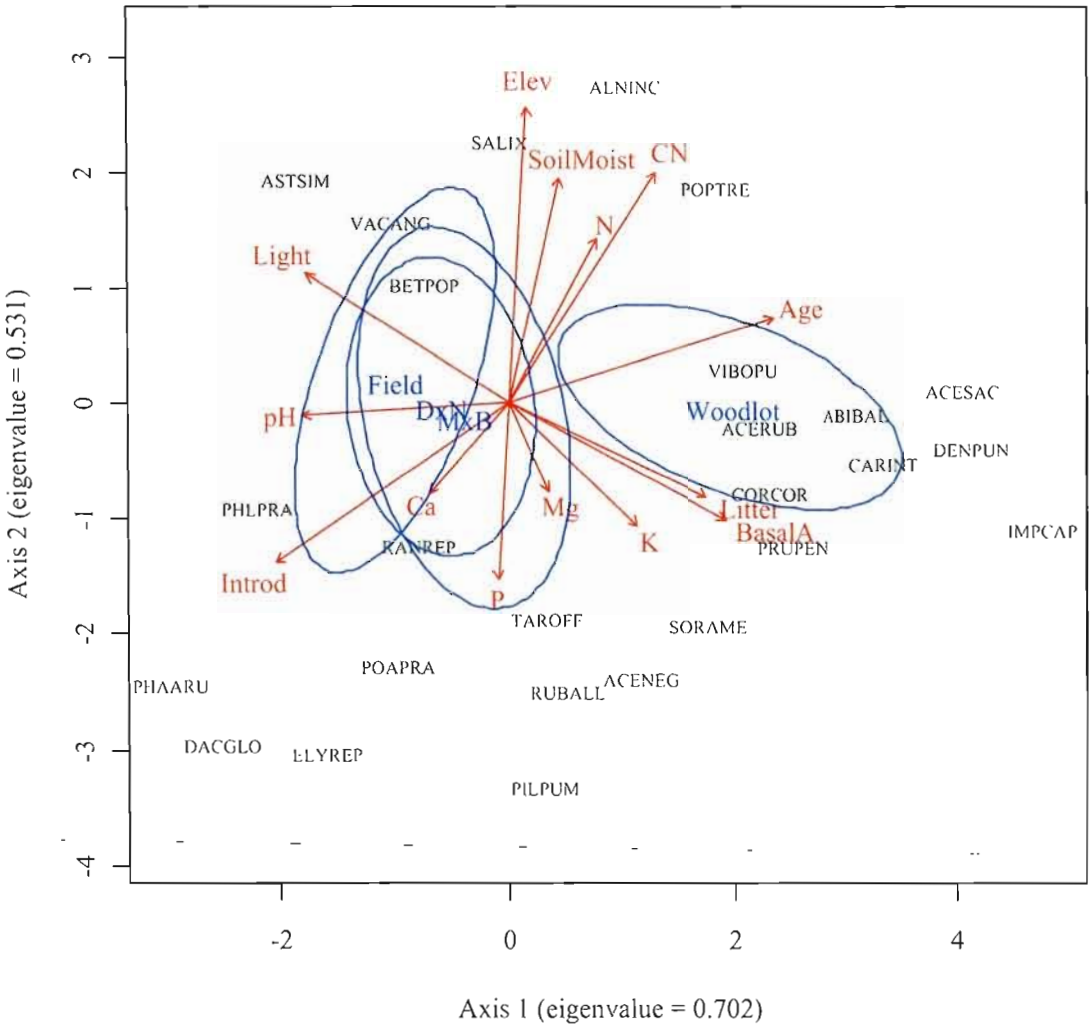

Figure 2.6 First two axes of a Detrended Correspondence Analysis of understory vegetation in plantations of two hybrid poplar clones, abandoned fields and natural woodlots at each of eight sites distributed across an elevation gradient. Environment centroids and 68% confidence interval ellipses are shown in blue (Field: abandoned field; DxN poplar: plantation of a DxN poplar clone; MxB poplar: plantation of an MxB poplar clone; Woodlot: second-growth hardwood woodlot). Fitted environmental attributes are shown in red (Elev: site elevation; P, K, Mg, Ca, N: soil nutrient and carbon concentrations; pH: soil pH; CN: soil C:N ratio; SoilMoist: soil moisture in August; Litter: leaf litter biomass in late fall, Age: time since last disturbance; BasalA: stand basal area; Light: light transmitted through the canopy, Introd: relative abundance of introduced species). A subset of species are shown in black.[1]

[1] ABIBAL: *Abies balsamea*, ACENEG: *Acer negundo*, ACERUB: *Acer rubrum*, ACESAC: *Acer saccharum*, ALNINC: *Alnus incana*, ASTSIM: *Aster lanceolatus*, BETPOP: *Betula populifolia*, CARINT: *Carex intumescens*, CORCOR: *Corylus cornuta*, DACGLO: *Dactylis glomerata*, DENPUN: *Dennstaedtia punctilobula*, ELYREP: *Elytrigia repens*, IMPCAP: *Impatiens capensis*, PHAARU: *Phalaris arundinacea*, PHLPRA: *Phleum pratense*, PILPUM: *Pilea pumila*, POAPRA: *Poa pratensis*, POPTRE: *Populus tremuloides*, PRUPEN: *Prunus pensylvanica*, RUBALL: *Rubus allegheniensis*, SALIX: *Salix* sp., SORAME: *Sorbus americana*, TAROFF: *Taraxacum officinale*, VACANG: *Vaccinium angustifolium*, VIBOPU: *Viburnum opulus*.

CHAPTER III

THE SUITABILITY OF HYBRID POPLAR PLANTATIONS AS HABITAT FOR NATIVE UNDERSTORY PLANTS: A TRANSPLANT EXPERIMENT

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Abstract

Multi-functional plantations using fast-growing tree species can potentially be used to accelerate the restoration of forest habitat on abandoned farmland. Such plantations may also be an interesting context for the cultivation of native plants as non-timber forest products. The present study used experimental introductions to assess the habitat value of ten-year-old plantations of two different hybrid poplar clones compared with natural secondary forests. Four species of native understory herbs with horticultural or medicinal value (*Trillium grandiflorum*, *Sanguinaria canadensis*, *Maianthemum racemosum,* and *Asarum canadense*) were transplanted as juveniles or adults into experimental plantations of two hybrid poplar clones and nearby woodlots at six sites in southern Quebec, Canada. The transplanted individuals were protected from deer browsing with cages. Survival, growth, and flowering were measured just after transplantation and after one year. *Trillium* survival was higher in the woodlots than in the plantations, while the other three species performed equally well or better in the plantations compared to the woodlots. In all cases, the differences in performance among sites were more important than the differences between environments. While these results are only preliminary, they suggest that cultivating forest understory species in hybrid poplar plantations could provide an interesting alternative to their cultivation in naturally regenerated woodlots, and especially to avoid any harvest from natural populations. They also suggest that any limitations on the spontaneous colonization of the hybrid poplar plantations by these understory plant species must operate at some other stage of their life cycle.

Keywords: Hybrid poplar plantations, abandoned farmland, understory, transplant, non-timber forest product, forest herbs

3.1 Introduction

In many landscapes of Europe and North America, the concentration and intensification of agriculture has resulted in the abandonment of less productive agricultural land, which is now in various stages of old field succession (Domon and Bouchard 2007; Le Houérou 1993; Poyatos et al. 2003; Roura-Pascual et al. 2005). The process of abandonment has been gradual, with the more marginal sites generally being abandoned first, and since reconverting to mature secondary forest (Domon and Bouchard 2007; Glitzenstein et al. 1990), while other, richer sites tended to be kept in production or in pasture until more recently and are currently at earlier stages of succession.

Recently abandoned farmland is of interest for active afforestation, in order to accelerate the return of a forest canopy (Chazdon 2008). Commercial plantations on abandoned farmland could increase the economic value of these lands through wood production, while at the same time restoring certain ecological functions (Paquette and Messier 2010). Since many species ranges are expected to shift as a result of climate change (Honnay et al. 2002), plantations may also be useful for restoring forest habitat connectivity in fragmented landscapes. Fast-growing tree species such as hybrid poplars, which are commonly planted in North America and Europe for wood fibre production, could be especially interesting in such projects, creating a tree cover from an existing field in the span of one to two decades (Marchand and Masse 2007).

It may also be possible to combine plantations with the commercial production of native plant species of horticultural or medicinal value as non-timber forest products (NTFPs). Native forest herb species are generally slow-growing and their harvest from wild populations is therefore often unsustainable (Charron and Gagnon 1991; Nantel et al. 1996; Nault and Gagnon 1993). Several understory species, including white trillium (*Trillium grandiflorum*), wild ginger (*Asarum canadense*), and bloodroot (*Sanguinaria canadensis*), are already listed as vulnerable in Quebec, due to risks of overexploitation of wild populations (Ministère du Développement Durable, de l'Environnement et des Parcs du Québec 2010). Their cultivation in plantation understories could provide a more sustainable

supply of these plants, as well as an additional and earlier return on investment for plantation owners.

While a plantation can create a tree cover on an old field very rapidly, it is important to understand whether the resulting environment can be suitable for native plant species adapted to forest understories. Plantation understories may differ from those of natural secondary forests as a result of site preparation disturbances, differences in tree species composition, reduced tree species richness, and simplified stand structure (Aubin et al. 2008). Hybrid poplar plantations in particular are often planted as monocultures and many of the commonly-used clones in North America have one or more exotic parent species. Hybrid poplar clones with different parent species may affect understory plants differently, with previous studies noting differences among species in terms of branching patterns and leaf biomass (Fortier et al. 2010), root density (Fischer et al. 2006), nitrogen cycling (Schimel et al. 1998) and understory vegetation biomass (Fortier et al. 2011). However, it is not known to what degree these factors affect native understory plants, and whether the understory environment of certain hybrid poplar plantations may be sufficiently similar to a forest understory to support populations of native forest herbs.

Experimental introductions have been used in secondary forests to directly test the suitability of the habitat for forest herb species (Brunet and Von Oheimb 1998; De Keersmaeker et al. 2004; Singleton et al. 2001). This approach can provide a synthetic measure of the various abiotic factors that combine to affect habitat quality, and can overcome the limitations of studying existing vegetation communities, which are often strongly influenced by dispersal. Baeten and colleagues (2009) used this approach to test the performance of four native understory species in hybrid poplar plantations in Belgium. They found that after eight years, the introduced populations of two of the species had declined over time in the plantations, but not in old-growth forests, an effect which was attributed to increased competition within the plantations. On the other hand, the other two forest species performed equally well in the plantations as in the old-growth forests.

The present study used experimental introductions as a preliminary assessment of the habitat value of ten-year-old plantations of two hybrid poplar clones compared with secondary

forests of natural origin. Four species of native understory herbs with horticultural or medicinal value were transplanted as juveniles or adults to simulate their reintroduction in a restoration context or their cultivation as NTFPs. The objectives of this study were (1) to compare the survival, growth, and flowering of transplanted understory plants in plantations of two clones of hybrid poplar and in secondary forest stands, and (2) to investigate the relationship between abiotic factors and the survival, growth, and flowering of these transplants.

3.2 Methods

3.2.1 Study area and plantation sites

The study took place in the Eastern Townships region of Quebec, Canada (Fig. 2.1), across a regional climatic gradient corresponding to an elevation gradient from the St. Lawrence Lowlands to the foothills of the Appalachian Mountains. This gradient spans three ecological regions: region 1a-T, at the lowest elevetations and with the mildest climate, with typical mature forest stands on mesic sites is being dominated by sugar maple and hickory (*Acer saccharum* - *Carya cordiformis*); region 2c-T, at mid-elevations, characterized by sugar maple - basswood (*Acer saccharum* - *Tilia americana*) stands; and finally region 3d-M, at the highest elevations, characterized by sugar maple - yellow birch (*Acer saccharum* - *Betula alleghaniensis*) stands. The landscapes of southern Quebec represent an excellent opportunity to study the multi-functional potential of tree plantations. Many regions have been largely deforested due to agriculture; however, agricultural activities have since been largely concentrated into the St. Lawrence Lowlands, resulting in the abandonment of many fields outside this region (Domon et Bouchard, 2007).

The present study uses a series of similar experimental hybrid poplar plantations, planted in May 2000 for a study on hybrid poplar establishment and growth at eight sites across the Eastern Townships (Truax and Gagnon, 2008). The site characteristics are summarized in Table 2.1. The plantations were all established on privately-owned fields that had been used for either grazing or crops, and subsequently abandoned. The vegetation before planting ranged from herbaceous to mixed herbaceous - shrub communities. Sites were prepared for

planting in the fall of 1999 by ploughing and disking, and resprouting or germinating vegetation was eliminated in June 2000 by an application of glyphosate herbicide over the entire plantation area. Following this treatment, 2 m long rooted cuttings of nine different hybrid poplar clones were planted by hand at each site at a stem density of 833 ha^{-1} (4 m between rows and 3 m between stems along the row). Glyphosate was again applied in June 2001, but only between the rows.

After ten seasons of growth, a wood volume production gradient had emerged across the sites. At certain sites, the plantations showed exceptional growth, while at others, they showed average or poor growth. The majority of these plantations had, however, developed a closed canopy. In this study, understory native herbaceous plants were planted in the six most successful of these plantations.

3.2.2 Experimental design

Each plantation contains three replicate 12 m x 12 m plots of each of nine hybrid poplar clones in a randomized block design. For this study we used only two of these clones, namely clone 915303, a hybrid of *Populus maximowiczii* and *P. balsamifera* (M x B), and clone 131, a hybrid of *P. deltoides* and *P. nigra* (D x N), both developed in Quebec. Clone 3333, another D x N hybrid, was used in place of clone 131 where the latter showed significant damage. Three forest control plots were selected in areas of secondary forest close to the plantations. These forested areas had regenerated naturally after either the harvest of a previous stand, or the abandonment of agriculture. The age of each stand was estimated based on cores taken from a sample of the largest trees and interviews with landowners. Three plots of 12 m x 12 m were selected from within these stands, located as near as possible to the plantations. Exceptionally, at the La Patrie (LAP) site, the three secondary forest plots were located 3.6 km from the plantation. Thus, the present study consists of three plots per site of secondary forest, and three plots per site of each of the M x B and the D x N hybrids, for a total of 54 plots (6 sites x 3 habitat types x 3 replicates)

We established experimental plantations of understory native herbaceous plants within each of the plots described above. We chose four species with ecological and economic value,

which could potentially serve as non-timber forest products (NTFPs). These are: *Asarum canadense* Linnaeus, *Maianthemum racemosum* (Linnaeus) Link (syn. *Smilacina racemosa*), *Sanguinaria canadensis* Linnaeus and *Trillium grandiflorum* (Michaux) Salisbury. All of these species, apart from *Maianthemum*, are officially designated as vulnerable species in Quebec, due to the threat of overexploitation of wild populations. *Asarum* has a good production potential because of its essential oils, while *Sanguinaria* is known for its production of sanguinarine, a powerful alkaloid with known medicinal uses. *Trillium* and *Asarum* are both valued for their ornamental value in shaded gardens. No natural populations of any of the transplanted species were present in any plot; however, a patch of *Asarum* was observed near to one of the plots in the Bromptonville woodland.

3.2.3 Transplantation

Seedlings of these four species were purchased from Horticulture Indigo, a specialized nursery that cultivates native plants from seed, thus avoiding an impact on wild populations. This nursery was located in Melbourne, at the centre of our study area, avoiding any unnecessary transportation time that could compromise plant quality. We chose to use seedlings because introductions of forest perennial herbs have been shown to be more successful from seedlings than from seed (Francis et al. 1992, Francis and Morton 1995, Primack 1996). We planted *Asarum* and *Maianthemum* in all 54 plots over the six sites. Due to the limited availability of plants, we planted *Sanguinaria* and *Trillium* at only three of the sites (27 plots). In each plot, we planted 10 individuals (*Trillium* and *Maianthemum*) or clumps (*Sanguinaria* and *Asarum*) of each species. Occasionally, 11 or 12 individuals of *Trillium* or *Maianthemum* were planted in cases in which it was impossible to separate two that had grown together. In total, 1636 plants were planted (Table 1). The plants were introduced into small rectangular understory plantations from which all understory vegetation, large surface roots (to 15 cm depth), and litter were removed by hand. These understory plantations consisted of two rows per species and five plants per row with a spacing of 20 cm between plants and 20 cm between the rows (total areas of 120 cm x 180 cm for four species, and 120 cm x 100 cm for two species).

The experimental plants were transplanted between May 25, 2009 and June 4, 2009. No weeding has been done since transplantation, but we protected the plants from larger herbivores (mostly white-tailed deer) with chicken-wire cages. Following transplantation, between June 10 and 18, 2009, we counted the leaves and flowers of each plant and measured the length of *Trillium* leaves as measures of the initial size of the plants in year 1 of the experiment. *Sanguinaria* flowers were not counted the first year because they had already finished flowering by the time they were transplanted. The following spring (2010), after one year of growth, the size of all surviving plants was again recorded. *Sanguinaria* flowers were counted on April 22 and 29, 2010 at the Bedford and Bromptonville sites respectively (lower elevation sites), and all remaining counts and measurements were taken between May 21 and June 3, 2010. Due to the rapid clonal spread of the *Asarum* plants at certain plots, the individuals became difficult to distinguish by year 2 (2010) of the experiment and were therefore measured as a single large "individual" at each plot.

3.2.4 Environmental characteristics

The environment within each plot was characterized during the 2009 growing season by its soil chemical and physical properties, stand basal area, light availability in the understory, and leaf litter biomass. Within each of the 54 plots, we collected five soil samples distributed systematically within the plot for chemical analysis. Samples were taken from the mineral soil at a depth of between 5 cm and 10 cm, between July 15, 2009 and August 6, 2009. This depth corresponds to the principal rooting zone of herbaceous plants. The five samples from each plot were combined into one, then air-dried and passed through a 2 mm sieve. The pH was measured in a suspension of one part soil in two parts water. The available potassium (K), calcium (Ca), and magnesium (Mg) contents were determined through extraction with $BaCl_2$ and detection by atomic absorption. The extractable phosphorus (P) content was measured using the Bray-2 method (Bray and Kurtz 1945) (modified by F. Lambert). The total nitrogen (N) and total carbon (C) were measured using dry combustion at 960°C, high-temperature reduction of the combustion products, and thermo-conductometric detection using a multi-elemental analyzer (vario MACRO, Elementar Analysensysteme GmbH, Hanau, Germany).

Soil moisture was sampled twice during the growing season, between June 23 and 26, 2009 and between August 14 and 15, 2009, corresponding to dry periods with no significant rainfall events recorded in the 48 hours prior. Samples were collected at a depth of 10 cm, one from the centre of each plot, in small metal containers. The moisture content was then determined gravimetrically after oven drying for 72 hours at 60°C.

Light availability at a height of 90 cm was measured once in each plot between July 15, 2009 and August 3, 2009. A digital hemispheric photo was taken at the centre of the plot and analyzed using the Gap Light Analyzer software, v. 2.0 (Frazer et al., 1999), to determine canopy openness and the average light received during the growing season.

Leaf litter biomass was measured between October 26, 2009 and November 4, 2009, after almost all the leaves had fallen from every tree. The leaf litter was collected from a 50 cm x 50 cm microplot at the centre of each plot and subsequently dried and weighed.

3.2.5 Analyses

Percent survival was calculated in each plot for *Maianthemum, Sanguinaria,* and *Trillium*. It was not possible to calculate survival for *Asarum* because the individual plants were not always distinguishable in year 2. As indicators of plant growth, the relative increase or decrease in each size measure was calculated for all surviving plants as the difference between year 2 and year 1 values divided by the year 1 value. For *Asarum*, the same growth indicators were calculated using the pooled data from all plants within a plot, which were treated as a single plant for the purpose of analyses. The proportion of *Trillium* juveniles passing into the three-leaf stage was also calculated as the number of three-leaf *Trillium* plants in year 2 that had had only one leaf the previous year, divided by the total number of surviving *Trillium* plants in year 2 that had one leaf in year 1. The relative increase in *Sanguinaria* flowers could not be calculated because data was not available for year 1 flowering. The number of *Sanguinaria* flowers observed in each clump year 2 was used in the analyses instead.

Separate analysis of variance tests (ANOVAs) were done on each response variable for each species. Response measures were subjected to log or arcsine-root transformations if the normality of ANOVA residuals and homoscedascicity were improved by doing so; for presentation purposes the raw data are used in figures and tables. The models for all ANOVAs included habitat type (three levels: DxN poplar plantation, MxB poplar plantation, and woodlot), site, and their interaction as fixed factors. For survival measures, *Asarum* response variables, and the proportion of *Trillium* juveniles passing into the three-leaf stage, the experimental unit was the plot (n = 3 per cell). For all other variables, plots were a random factor in the model, nested within habitat type and site, and the experimental unit was the individual plant (n = 10 per cell). Principal component analyses (PCA) were performed to assess the relationships among the various response variables and the principal gradients of variation. The first PCA used response variables for all four species at three sites (Bedford, Bromptonville, and La Patrie) and a second PCA used only *Asarum* and *Maianthemum* responses with data from all six sites. Both PCAs were fitted with the measured environmental variables. Species variables and environmental variables were standardized prior to analysis. The JMP software package (SAS Institute, Cary, NC) was used for all ANOVAs and the vegan package in R was used for PCAs (Oksanen et al. 2010).

3.3 Results

3.3.1 General results of transplant experiment

The four species planted in year 1 varied considerably in initial size. None of the *Trillium grandiflorum* or *Maianthemum racemosum* plants were at reproductive maturity and 72% of *Trillium* plants were seedlings with just one leaf. *Maianthemum* plants had between one and seven leaves each (mean ± s.d. = 3.34 ± 1.23). *Sanguinaria canadensis* plants were somewhat larger at the time of transplanting; many showed evidence of flowering earlier that spring, although flowers were not counted for year 1. *Sanguinaria* was planted as clumps with an initial size of one to four leaves (mean ± s.d. = 1.40 ± 0.74). *Asarum canadense* plants were the largest of the four species and all clumps contained mature, flowering individuals.

In year 2 (one year after transplanting), average survival rates by plot were 69% ± 27% (standard deviation) for *Maianthemum*, 83% ± 21% for *Sanguinaria*, and 75% ± 20% for *Trillium*. Of the surviving one-leaved *Trillium* seedlings, 58% had progressed to the three-leaf adult stage by the second year. Survival was not calculated for *Asarum* plants, but clumps showed on average a decline in size in the first year from 93 to 80 leaves, corresponding to a decrease of 17% ± 35% (s.d.). Damage from slugs and other invertebrates was evident in many plots for all of these species, although this damage was not quantified. All but one of the 54 *Asarum* clumps produced flowers in year 2, while 44% of *Sanguinaria* clumps and only one *Trillium* plant flowered the second spring. None of the *Maianthemum* plants flowered in either year.

3.3.2 Effects of site and type of environment

The results of the ANOVAs show that site had a greater effect on the experimental plants than the type of environment (Table 3.2). Site had the largest effect on all variables, except for the increase in the number of *Sanguinaria* leaves, for which no effect was significant. Environment-site interaction effects were also significant for most variables, and for some the interactions were close behind site effects in importance.

Environment had a significant effect on *Asarum* clump size ($p < 0.05$), but not flowering, with the number of leaves decreasing less over the first year in the MxB poplar plantations than in the woodlots (Table 3.3). *Maianthemum* survival and growth were not significantly different across the three environments, although there was a trend toward higher survival rates in the MxB plantations than in the woodlots (Table 3.3). *Sanguinaria* survival and growth did not differ across the three environments, but the clumps did produce significantly more flowers in the plantations than in the woodlots (Table 3.3). In contrast to the other species, *Trillium* showed an overall poorer response in the plantations compared to the woodlots. Survival was significantly affected by the type of environment, and was lower in the DxN plantations than in the woodlots (Table 3.3). Also, *Trillium* seedlings were less likely to progress to the three-leaf stage in the MxB plantations than in the woodlots (Table 3.3). No significant differences were detected between the two poplar clones, although there

is a trend toward higher survival rates among *Sanguinaria* and *Trillium* plants in plantations of the MxB clone, while more of the surviving *Trillium* seedlings progressed to the three-leaf stage in plantations of the DxN clone (Table 3.3).

Site effects were important for all four species, and for *Asarum* and *Sanguinaria*, this effect can be in part attributed to the site elevation gradient (Figs. 3.2 and 3.3, respectively). Both of these species tended to perform better at lower elevation sites, with a significant correlation for the increase in *Asarum* leaves ($r^2 = 0.211$, $p < 0.001$) and flowers ($r^2 = 0.383$, $p < 0.001$) and *Sanguinaria* flowering in year 2 ($r^2 = 0.414$, $p < 0.001$), but not for *Sanguinaria* survival ($r^2 = 0.115$, $p = 0.083$) or growth ($r^2 = 0.046$, $p = 0.281$). The Bedford site, situated in the St. Lawrence Valley lowlands at the lowest elevation of the six sites, was the only site at which *Asarum* clumps increased in size (Fig 3.2). On the other hand, neither *Maianthemum* nor *Trillium* showed any obvious trends along the elevation gradient (Figs. 3.2 and 3.3, respectively).

3.3.3 Response of transplants along environmental gradients

The principal components analyses (PCAs) identified the most important gradients along which survival, growth and flowering of the species varied. In the three-site subset in which all four species were present (Fig 3.4), each species responded slightly differently to the environment. The first principal component accounted for 35.3% of the variation and was associated with decreasing success of *Asarum, Trillium,* and *Maianthemum*, but not of *Sanguinaria*. This first axis was not significantly correlated with any of the measured environmental characteristics of the plots, indicating that some other, unmeasured aspect of the environment had an important influence on these plants. The second axis (27.7%) was associated with increasing growth and especially increasing flowering of *Sanguinaria* and *Asarum*, and decreasing survival of *Trillium*. *Maianthemum* growth was also slightly higher at the negative end of this gradient. This axis was correlated most strongly with decreasing elevation ($r^2 = 0.593$, $p < 0.001$) and decreasing soil moisture in June ($r^2 = 0.449$, $p < 0.001$). When only *Asarum* and *Maianthemum* were considered across all six sites, the first principal component explained 54.0% of the variability and was correlated with decreasing *Asarum*

growth and flowering, and decreasing *Maianthemum* survival (Fig. 3.5). The second principal component explained 27.7% of the variability and was associated with decreasing survival and growth of *Maianthemum* plants. Of the measured environmental variables, the first axis was most strongly correlated with increasing soil moisture in June ($r^2 = 0.370$, $p < 0.001$) and August ($r^2 = 0.240$, $p < 0.001$), as well as decreasing soil P ($r^2 = 0.204$, $p < 0.001$) and increasing elevation ($r^2 = 0.195$, $p = 0.001$). The second axis was most strongly correlated with increasing soil Mg ($r^2 = 0.213$, $p < 0.001$) and decreasing elevation ($r^2 = 0.149$, $p = 0.005$). Neither basal area nor light were significant when fit to the first two axes of either ordination.

Both the three-site and six-site PCAs suggest that the response of *Asarum* plants was best at lower elevations and in drier soils (Figs. 3.4 and 3.5), which is confirmed by linear regressions of *Asarum* growth as a function of elevation ($r^2 = 0.211$, $p < 0.001$) and June soil moisture ($r^2 = 0.400$, $p < 0.001$) and of flowering as a function of these two variables ($r^2 = 0.383$, $p < 0.001$ and $r^2 = 0.390$, $p < 0.001$, respectively). *Maianthemum* survival was not strongly correlated with any measured variable in either PCA, but its growth appeared to be stronger at higher elevations and in less Mg-rich soils, although follow-up regressions showed that Mg was only weakly, but significantly, correlated with *Maianthemum* growth ($r^2 = 0.175$, $p = 0.002$) while the correlation with elevation was not significant ($r^2 = 0.064$, $p = 0.071$). The three-site PCA suggests that *Sanguinaria* flowering was associated with a number of the measured environmental variables and follow-up linear regressions confirmed that the number of flowers in *Sanguinaria* clumps was correlated with decreasing elevation ($r^2 = 0.414$, $p < 0.001$), decreasing C:N ratio ($r^2 = 0.262$, $p = 0.006$), decreasing soil moisture in June ($r^2 = 0.338$, $p = 0.003$), and increasing soil available P ($r^2 = 0.165$, $p = 0.036$). However, flowering was not significantly correlated to leaf litter biomass ($r^2 = 0.051$, $p = 0.256$) or soil pH ($r^2 = 0.062$, $p = 0.212$), Ca ($r^2 = 0.082$, $p = 0.148$), or Mg ($r^2 = 0.117$, $p = 0.081$). *Sanguinaria* growth was not strongly correlated with either of the first two principal components and was more strongly associated with the third (not shown); however, no measured environmental variables were significantly correlated with this axis. *Trillium* survival was negatively correlated with soil Mg ($r^2 = 0.252$, $p = 0.008$) and pH ($r^2 = 0.155$, $p = 0.042$), but not with Ca ($r^2 = 0.079$, $p = 0.156$), and there was a trend towards a positive correlation with leaf litter biomass ($r^2 = 0.125$, $p = 0.071$). Unlike the other three species, the

growth of *Trillium* plants was not positively correlated with its survival; in fact, the proportion of surviving seedlings progressing to the three-leaf stage was strongly negatively correlated with survival. *Trillium* leaf size was not strongly correlated with any measured variables.

3.4 Discussion

3.4.1 Transplant success

The *Trillium* and *Maianthemum* plants showed the highest mortality in the first year, probably because of their small size, which is believed to be the largest single source of transplant shock (Vasseur and Gagnon 1994). However, already during the first year, transplants respond to their environment, allowing preliminary conclusions to be drawn regarding the comparative suitability of the different environments in which the transplants were planted (Vasseur and Gagnon 1994).

After one year, the *Asarum*, *Sanguinaria*, and *Maianthemum* plants in this study survived and grew on average equally well in the plantations, compared to the naturally regenerated woodlots. *Sanguinaria* plants also showed a trend toward better survival in the plantations than in the woodlots. On the other hand, the *Trillium* plants were generally less successful in the plantations than in the woodlots, but still showed a capacity for survival and growth in the plantations.

The four species each responded somewhat differently to the environments, indicating different niches. *Asarum* and *Sanguinaria* grew better at lower elevations, which is to be expected since both these species are near the northern edges of their range (Kiger 1997; Whittemore et al. 1997). *Maianthemum* and *Trillium*, on the other hand, showed no obvious preference along the elevation gradient. In the case of *Maianthemum*, this result is explained by the fact that *Maianthemum* is a somewhat more northerly species than either *Asarum* or *Sanguinaria* (LaFrankie 2002). However, for *Trillium*, the opposite is true: the range of this species extends less into the north than any of the other three species (Case 2002), and the La Patrie site is actually outside of its natural range (Québec 2005). It is therefore not apparent

why *Trillium* plants were able to survive and grow equally well at the La Patrie site as at the two lowest elevation sites. *Asarum* and *Sanguinaria* also responded best in better drained, rich soils. This result is in agreement with the habitat descriptions given for these species in a Quebec Flora as "rich woods" (Frère Marie-Victorin 1995). Both of these species are also listed as indicator species for the rich mesic forest type in New Hampshire (New Hampshire Department of Resources and Economic Development). On the other hand, *Trillium* is also typically described as growing in "rich" environments (Case 2002; Québec 2005), yet in our study the *Trillium* plants were more likely to survive in more acidic soils with lower Mg concentrations. Shading was not a significant factor in this study for explaining the differences in survival, growth and flowering among the plots. This result is not surprising when only the three most productive plantations are considered, along with their neighbouring woodlots, since the variation in light levels in the understory is small within this subset of sites. However, when all six sites were considered, a larger range of light conditions was apparent, with 9.9% to 41.4% canopy openness. At the more open end of this gradient, we can hypothesize that there may be negative effects of increased competition that will only become apparent in later years, once the competing vegetation fully recovers from the site-preparation that was effected prior to transplanting.

Much of the variability observed in this study in survival, growth, and flowering was not explained by any of the measured environmental variables, indicating that other, unmeasured variables played an important role. One variable that may have played a role in the difference in responses among sites (which was an important difference for all transplant response variables) was the weather conditions under which the transplants were planted. since each site was planted on a different day. Because the transplants were not watered after planting, a lack of soil moisture could have been a factor in the degree of initial transplanting shock. Other, unmeasured factors such as the abundance of slugs and other invertebrate herbivores, topography, land-use history, or competition may also have contributed to the variability among plots, contributing to both site and site-environment interaction effects. Although deer are generally the most important herbivores for forest understory species (Whigham 2004), the effect of small herbivores, particularly slugs, was potentially important, as noted anecdotally in this study and in a previous study on *Asarum* in southern Ontario (Liang 2009). Below-ground herbivores can also play an unobserved role in mortality or in

limiting growth (Hunter 2001). These effects were likely particularly important for *Trillium* and *Maianthemum*, explaining the weak correlations with the measured environmental variable in this study and the inconsistencies between the results of this study and the typical habitat descriptions for these species. This may be due to their small initial size, compared to larger *Asarum* and *Sanguinaria* plants, which would have made them more vulnerable to weather conditions, small herbivore damage, and any other stochastic factors.

The negative correlation observed in *Trillium* between survival and proportion of seedlings maturing is most likely because mortality during the first year was higher among the smaller and weaker seedlings than the larger ones, while the larger seedlings were more likely to progress to the three-leaf stage the following year. This produces the statistical artifact of a higher proportion of the *surviving* seedlings progressing to the three-leaf stage in plots where mortality was high and many of the smaller seedlings were killed off.

3.4.2 Ecological implications

The success after one year of the transplants in the hybrid poplar plantations is preliminary evidence for the suitability of certain hybrid poplar plantation environments for these four species of forest understory plants. However, the survival and growth of the understory plants should be assessed over many years to determine if the trends observed in the first year are maintained. One factor that may come into play in subsequent years is an increase in competition due to the recovery of the competing vegetation after having been cleared prior to transplanting. In plots with more open canopies, grasses and other field-adapted species may take several years to re-invade the site, causing a decline of the transplants with increasing competition. The re-expansion of the hybrid poplar root system may also play a role, since these roots were partly removed from the planting area prior to transplanting. The MxB clone had a much denser root system than the DxN clone (K. Boothroyd-Roberts, field observations), the effects of which could create a difference in survival and growth between the two plantation environments in later years. It has also been suggested that secondary chemicals in *Populus balsamifera* litter can reduce nitrogen availability for other plant species (Schimel et al. 1998), and the MxB poplar clone, with this species as a parent, may

also have such an effect. Litter was removed prior to transplanting, but its compounds (tannins and phenols) may have already been incorporated into the soil.

Different weather conditions in later years may also expose vulnerabilities of the transplanted plants in one environment or another. For example, the difference in measured soil moisture between the plantations and the woodlots may become more critical in drier years, when a more severe summer drought could result in a rise in mortality in the plantations, compared to the woodlots.

The results of this study are also silent as to the suitability of the hybrid poplars plantations for other stages of the life cycle of these understory plant species, since forest herb species are often more vulnerable to environmental stresses at the seedling emergence and establishment stages (e.g., Bierzychudek 1982; Inghe and Carl Olof 1985; Nault and Gagnon 1993). Competition may, for example, inhibit the colonization of certain plantations by these species from seed, even though the mature plants were able to persist and grow well once established. Such a situation was suggested in populations of native forest herbs in hybrid poplar plantations in Belgium (Endels et al. 2004). A lack of soil moisture may also be more limiting at the seedling emergence phase than for adult plants due to a less developed and shallower root system (Albrecht and McCarthy 2009; Inghe and Carl Olof 1985; Nault and Gagnon 1993). Long-term monitoring is therefore needed to assess the viability of understory herb populations introduced into hybrid poplar plantations.

Large-animal herbivory may also be a barrier for understory plant species when not protected artificially by cages as was the case in this study. It has been noted in previous studies that an over-abundant population of whitetail deer (*Odocoileus virginianus*), such as has been observed in certain areas of southern Quebec, can seriously impair restoration efforts of understory herb populations (Lubbers and Lechowicz 1989; Ruhren and Handel 2003; Whigham 2004).

If these preliminary results are confirmed over longer-term studies, then it can be deduced that the major limitation to colonization of this new environment by understory plants is in the dispersal and/or seedling emergence or establishment stages, rather than in the suitability of the habitat itself for mature plants. If the limitation is dispersal, this barrier can be

overcome through intentional introductions as part of a forest ecosystem restoration project. Understory herbaceous plants could be transplanted into plantations as was done in this study and given a chance to establish while benefiting from protection from large herbivores and an initial elimination of the competition. This model of forest restoration would be especially interesting for the rapid creation of habitat corridors to link existing woodlots across agro-forested landscapes.

3.4.3 Implications for non-timber forest product cultivation

The results of this study suggest that it may be feasible to cultivate understory forest plants in plantations such as the hybrid poplar plantations in this study. More research is needed to evaluate the profitability of non-timber forest product (NTFP) production in hybrid poplar plantations, in comparison with other land-use options. This would depend on an assessment of the long-term productivity of these plants, as well as the initial costs of the plant material. Several authors have suggested that transplanting adult plants is more likely to be successful than planting seeds, since seedlings and juveniles are generally more vulnerable to the environment than are adult plants (Mottl et al. 2006; Ruhren and Handel 2003; Vasseur and Gagnon 1994). However, planting larger plants also carries a greater initial cost than planting from seedlings or seed. Also, the long-term feasibility of NTFP production in plantations still needs to be assessed in relation to plantation maintenance activities (pruning, thinning, harvesting and replanting). If partial harvests are carried out in winter, with a protective snow cover, the production of understory plants could potentially co-exist with wood production in a plantation. These preliminary results suggest that cultivating forest understory species in hybrid poplar plantations could provide an interesting alternative to their cultivation in naturally regenerated woodlots and especially to their harvest from natural populations. Three of the transplanted species (*Asarum*, *Sanguinaria*, and *Trillium*) are officially designated as vulnerable in Quebec because of the threat that harvesting from natural populations represents.

3.5 Conclusions

This study shows that it is possible for forest understory plants to survive and grow under a hybrid poplar plantation that only ten years earlier was an open field. While still preliminary, this result indicates the possibility of using hybrid poplars, or more generally, fast-growing hardwood trees, to quickly recreate an understory-like environment on an abandoned field that can then be used for ecological restoration or NTFP production.

Although the results obtained may not be generalizable everywhere, they are probably applicable to many regions of northeastern North America. It is likely that many landowners in this region could achieve similar results on abandoned farmland on their properties. For a landowner interested in practising forestry, cultivating non-timber forest products, or restoring a high-value forest ecosystem, the afforestation of an abandoned field may potentially be a more interesting option than using existing woodlots, which on many properties are on poorly drained land or land of otherwise little value. This option becomes especially useful at lower elevations, where land-use pressure from agriculture is stronger and existing woodlots are rarer and more likely to be of poor quality. The lower elevations are also where hybrid poplars can grow the most rapidly and where the restoration of a closed canopy is entirely feasible within a decade.

3.6 References

Albrecht, M.A. and B.C. McCarthy. 2009. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. Journal of Ecology **97**(5): 1037-1049.

Aubin, I., C. Messier and A. Bouchard. 2008. Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biological Conservation **141**(10): 2461-2476.

Baeten, L., M. Hermy and K. Verheyen. 2009. Environmental limitation contributes to the differential colonization capacity of two forest herbs. Journal of Vegetation Science **20**(2): 209-223.

Bélanger, L. and M. Grenier. 2002. Agriculture intensification and forest fragmentation in the St. Lawrence valley, Québec, Canada. Landscape Ecology **17**(6): 495-507.

Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: A Review. New Phytologist **90**(4): 757-776.

Brunet, J. and G. Von Oheimb. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology **86**(3): 429-438.

Case, F.W.J. 2002. *Trillium grandiflorum*. Flora of North America North of Mexico. Flora of North America Editorial Committee. New York and Oxford. **26**.

Charron, D. and D. Gagnon. 1991. The demography of northern populations of *Panax quinquefolium* (American Ginseng). Journal of Ecology **79**(2): 431-445.

Chazdon, R.L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science **320**(5882): 1458-1460.

De Keersmaeker, L., L. Martens, K. Verheyen, M. Hermy, A. De Schrijver and N. Lust. 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). Forest Ecology and Management **188**(1-3): 291-304.

Domon, G. and A. Bouchard. 2007. The landscape history of Godmanchester (Quebec, Canada): Two centuries of shifting relationships between anthropic and biophysical factors. Landscape Ecology **22**(8): 1201-1214.

Endels, P., D. Adriaens, K. Verheyen and M. Hermy. 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. Ecography **27**(2): 225-241.

Fischer, D., S. Hart, B. Rehill, R. Lindroth, P. Keim and T. Whitham. 2006. Do high-tannin leaves require more roots? Oecologia **149**(4): 668-675.

Fortier, J., D. Gagnon, B. Truax and F. Lambert. 2010. Biomass and volume yield after 6 years in multiclonal hybrid poplar riparian buffer strips. Biomass and Bioenergy **34**(7): 1028-1040.

Fortier, J., D. Gagnon, B. Truax and F. Lambert. 2011. Understory plant diversity and biomass in hybrid poplar riparian buffer strips in pastures. New Forests (in press).

Frère Marie-Victorin, É.C. 1995. Flore Laurentienne. Montréal, Les Presses de l'Université de Montréal.

Glitzenstein, J.S., C.D. Canham, M.J. McDonnell and D.R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bulletin of the Torrey Botanical Club **117**(2): 106-122.

Honnay, O., K. Verheyen, J. Butaye, H. Jacquemyn, B. Bossuyt and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters **5**(4): 525-530.

Hunter, M.D. 2001. Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. Agricultural and Forest Entomology **3**(1): 3-9.

Inghe, O. and T. Carl Olof. 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943-1981. Oikos **45**(3): 400-420.

Kiger, R.W. 1997. *Sanguinaria canadensis*. Flora of North America North of Mexico. Flora of North America Editorial Committee. New York and Oxford. **3**.

LaFrankie, J.V. 2002. *Maianthemum racemosum*. Flora of North America North of Mexico. Flora of North America Editorial Committee. New York and Oxford. **26**.

Le Houérou, H.N. 1993. Land degradation in Mediterranean Europe: can agroforestry be a part of the solution? A prospective review. Agroforestry Systems **21**(1): 43-61.

Liang, Y. 2009. Relationship between shade and herbivory in *Asarum canadense* (wild ginger). University of Toronto Journal of Undergraduate Life Sciences **3**.

Lubbers, A.E. and M.J. Lechowicz. 1989. Effects of leaf removal on reproductions vs. belowground storage in *Trillium grandiflorum*. Ecology **70**(1): 85-96.

Marchand, P.P. and S. Masse. 2007. Boisement et agroforesterie en courtes rotations en territoire privé au Québec : Examen des lois, règlements, politiques et programmes, Ressources naturelles Canada, Service canadien des forêts, Centre de foresterie des Laurentides.

Ministère du Développement durable, de l'Environnement et des Parcs du Québec. 2010. Plantes menacées ou vulnérables au Québec. Retrieved December 11, 2010, from http://www.mddep.gouv.qc.ca/biodiversite/especes/.

Mottl, L.M., C.M. Mabry and D.R. Farrar. 2006. Seven-year survival of perennial herbaceous transplants in temperate woodland restoration. Restoration Ecology **14**(3): 330-338.

Nantel, P., D. Gagnon and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology **10**(2): 608-621.

Nault, A. and D. Gagnon. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. Journal of Ecology **81**(1): 101-119.

New Hampshire Department of Resources and Economic Development, Division of Forests and Lands. Rich mesic forest system. Retrieved December 7, 2010, from http://www.nhdfl.org/about-forests-and-lands/bureaus/natural-heritage-bureau/photo-index/SystemPhotos/richmesicforest.aspx.

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens and H. Wagner. 2010. Vegan: community ecology package, version 1.17-4. R project for statistical computing.

Paquette, A. and C. Messier. 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment **8**(1): 27-34.

Peterken, G.F. 2000. Rebuilding networks of forest habitats in lowland England. Landscape Research **25**(3): 291-303.

Poyatos, R., J. Latron and P. Llorens. 2003. Land use and land cover change after agricultural abandonment: The case of a Mediterranean Mountain area (Catalan Pre-Pyrenees). Mountain Research and Development **23**(4): 362-368.

Roura-Pascual, N., P. Pons, M. Etienne and B. Lambert. 2005. Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. Mountain Research and Development **25**(3): 252-261.

Ruhren, S. and S.N. Handel. 2003. Herbivory constrains survival, reproduction and mutualisms when restoring nine temperate forest herbs. Journal of the Torrey Botanical Society **130**(1): 34-42.

Schimel, J.P., R.G. Cates and R. Ruess. 1998. The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan Taiga. Biogeochemistry **42**(1): 221-234.

Singleton, R.,S. Gardescu,P.L. Marks and M.A. Geber. 2001. Forest herb colonization of postagricultural forests in central New York State, USA. Journal of Ecology **89**(3): 325-338.

Truax, B. and D. Gagnon. 2008. Mesurage après 8 ans et élaboration d'équations prédictives de rendement de peuplier hybrides plantés en friches d'origine agricole en Estrie. Rapport final, Table des MRC de l'Estrie, Programme Volet II (projet E07-51), 19pp.

Truax, B., D. Gagnon, J. Fortier and F. Lambert. Biomass and volume yield after 8 years in multi-clonal hybrid poplar plantations on abandoned agricultural land along a climatic gradient in southern Quebec, Canada (in preparation).

Vasseur, L. and D. Gagnon. 1994. Survival and growth of *Allium tricoccum* Ait. transplants in different habitats. Biological Conservation **68**: 107-114.

Whigham, D.F. 2004. Ecology of woodland herbs in temperate deciduous forests. Annual Review of Ecology, Evolution, and Systematics **35**: 583-621.

Whittemore, A.T., M.R. Mesler and K.L. Lu. 1997. *Asarum canadense*. Flora of North America North of Mexico. Flora of North America Editorial Committee. New York and Oxford. **3**.

Table 3.1 Characteristics of the six hybrid poplar plantation study sites in the Eastern Townships region of Quebec, Canada

					Woodlot	Field and plantation				
Plantation sites (abbreviations)	Elevation (m)	Temperature: Mean annual (°C)	Degree days (>5°C)	Precipitation: Mean annual (mm)	Minimum stand age (yrs)	Estimated age since abandonment (yrs)	Clay ($g\ kg^{-1}$)	Silt ($g\ kg^{-1}$)	Sand ($g\ kg^{-1}$)	Textural class
Bedford (BED)	80	6.0	2061.3	1156.2	29 - 54	12	183	267	550	Sandy loam
Brompton (BRO)	170	5.3	1884.1	1149.8	34	5 - 10	287	517	197	Clay Loam
Ste-Catherine (CAT)	230	5.3	1859.9	1134.5	21 - 42	25	123	453	423	Loam
Ogden (OGD)	260	5.1	1805.6	1155.6	39	25	130	480	390	Loam
St-Adrien (ADR)	320	4.0	1648.5	1198.7	38	25	117	450	433	Loam
La Patrie (LAP)	440	3.7	1582.8	1297.5	58	12	123	553	323	Silty loam

Table 3.2 Fixed effects of ANOVAs (F and p values) on survival and growth measurements of four native understory species transplanted into three types of environments: plantations of two clones of hybrid poplar and second-growth hardwood woodlots

	Site		Environment		Interaction	
Variable	F	p	F	p	F	p
Asarum canadense						
Relative increase in total number of leaves per plot	16.61	<0.001**	4.43	0.019*	3.26	0.004**
Relative increase in number of flowers	10.82	<0.001**	1.08	0.351	3.04	0.007**
Maianthemum racemosum						
Survival	3.73	0.008**	0.44	0.646	1.76	0.105
Relative increase in number of leaves per surviving plant	5.53	0.001**	0.35	0.708	3.48	0.003**
Sanguinaria canadensis						
Survival	12.50	<0.001**	3.34	0.058	9.54	<0.001**
Relative increase in number of leaves per surviving plant	0.88	0.429	1.53	0.240	0.51	0.727
Number of flowers per plant in year 2	14.39	<0.001**	6.46	0.006**	3.49	0.025*
Trillium grandiflorum						
Survival	10.83	0.001**	3.54	0.050*	9.29	<0.001**
Proportion of year 1 one-leaf plants passing into the three-leaf stage in year 2	7.66	0.004**	4.06	0.035*	7.64	0.001**
Relative increase in leaf size	6.15	0.009**	1.40	0.270	1.91	0.151

Note: *Asarum canadense* and *Maianthemum racemosum* were planted at six sites, while *Sanguinaria canadensis* and *Trillium grandiflorum* were planted at three sites.
* Significance at $p < 0.05$
** Significance at $p < 0.01$

Table 3.3 First year survival and growth and environment effects (p-values) of four species of juvenile understory plants transplanted into three types of environments: plantations of two clones of hybrid poplar and second-growth hardwood woodlots

Variable	Hybrid poplar plantation				Second-growth hardwood woodlot		p-value of environment effect
	DxN clone		MxB clone				
	mean ± s.e.	n	mean ± s.e.	n	mean ± s.e.	n	
Asarum canadense							
Relative increase in total leaves per plot	-12 ± 10% (ab)	18	-10 ± 7% (a)	18	-28 ± 7% (b)	18	0.019*
Relative increase in total flowers per plot	32 ± 21%	18	30 ± 22%	18	-8 ± 14%	18	0.351
Maianthemum racemosum							
Survival	64 ± 7%	18	71 ± 6%	18	72 ± 6%	18	0.646
Relative increase in leaves per plant	30 ± 9%	116	23 ± 6%	127	25 ± 5%	129	0.708
Sanguinaria canadensis							
Survival	83 ± 7%	9	90 ± 6%	9	76 ± 8%	9	0.058
Relative increase in leaves per plant	53 ± 13%	75	68 ± 10%	81	29 ± 12%	68	0.240
Flowers per plant (year 2)	6.78 ± 1.75 (a)	75	6.33 ± 1.40 (a)	81	2.00 ± 0.47 (b)	68	0.006**
Trillium grandiflorum							
Survival	67 ± 8% (b)	9	78 ± 6% (ab)	9	80 ± 5% (a)	9	0.050*
Proportion of year 1 one-leaf plants passing into the three-leaf stage in year 2	65± 9% (ab)	9	53± 4% (b)	9	69± 9% (a)	9	0.035*
Relative increase in leaf size	84 ± 9%	60	82 ± 8%	70	71 ± 4%	72	0.270

Notes: Relative increases are calculated as: (Year 2 value – Year 1 value) / Year 1 value.
P-values are from ANOVAs with site and environment as fixed effects (see text for details).
Different letters indicate significant differences between environments at $p \leq 0.05$ in Tukey HSD means comparisons tests.
* Significance at $p \leq 0.05$
** Significance at $p \leq 0.01$

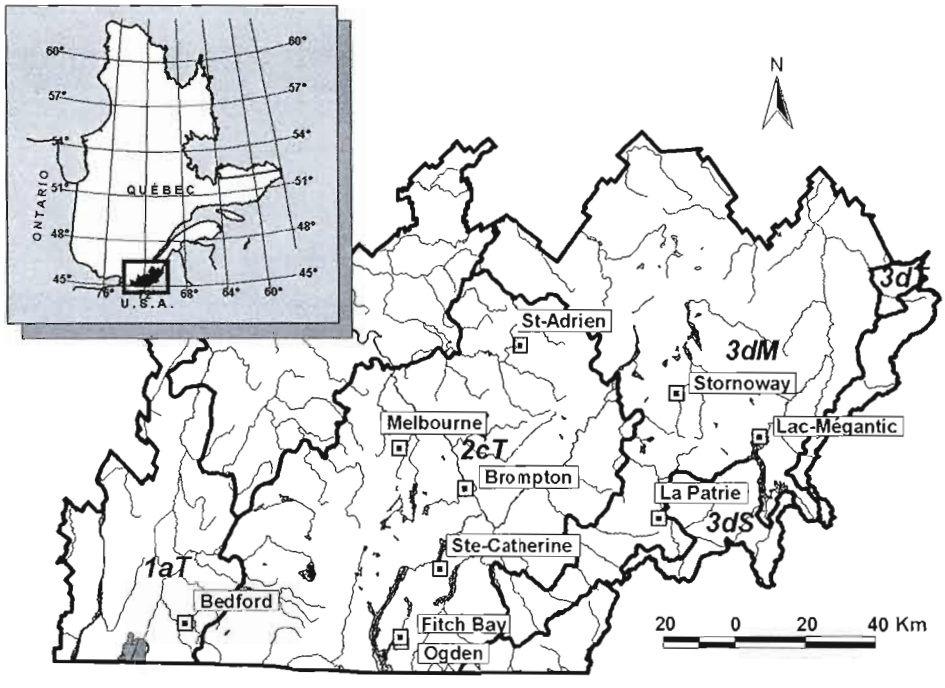

Figure 3.1 Study sites in the Eastern Townships region of Quebec, Canada. Ecological zones are also indicated (see text for details). The Melbourne, Fitch Bay, Stornoway, and Lac-Mégantic sites were excluded from this study.

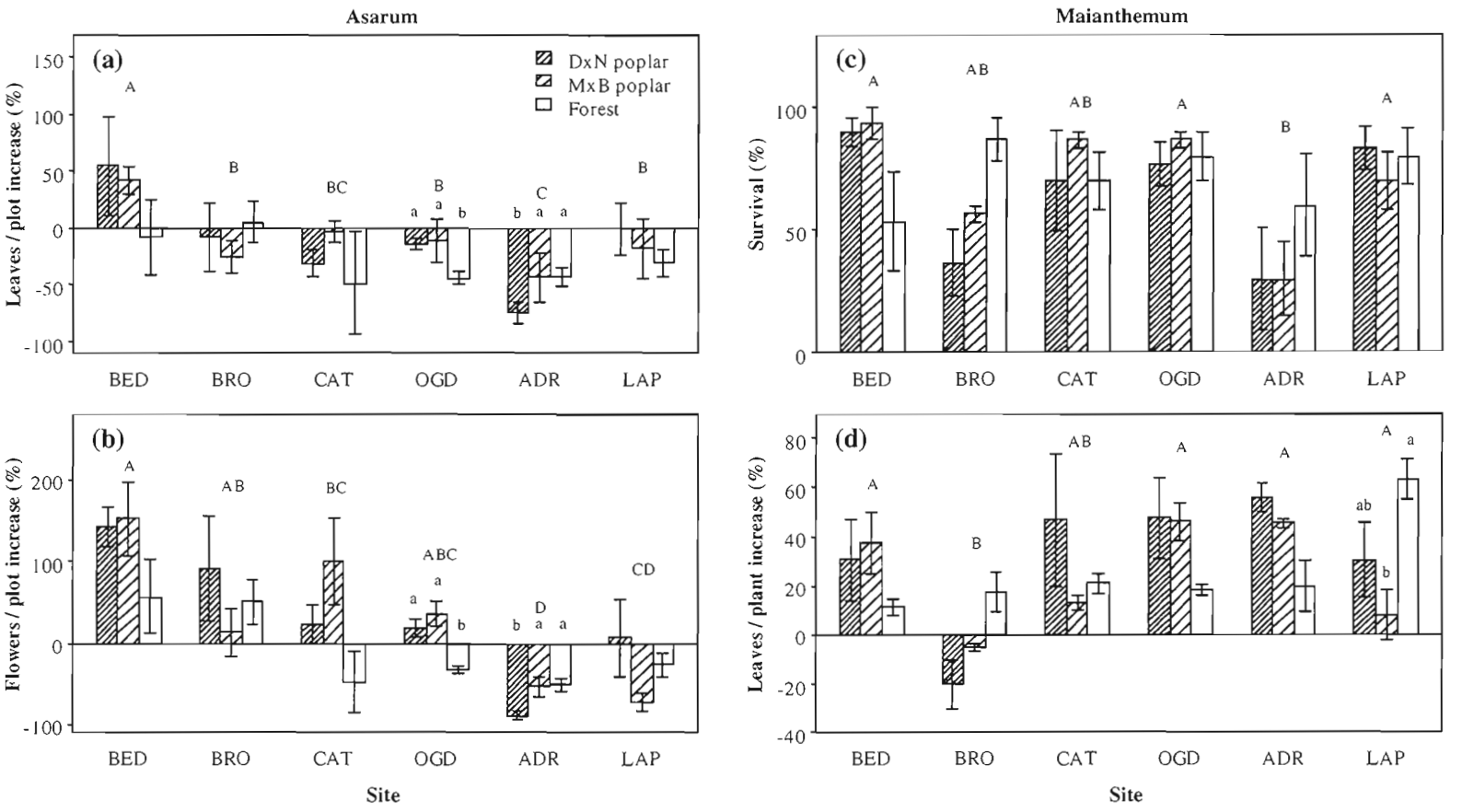

Figure 3.2 Responses of *Asarum canadense* and *Maianthemum racemosum* one year after transplantation into plantations of two hybrid poplar clones and natural woodlots at six sites. Increases in (a) number of leaves and (b) flowers of *Asarum* clumps; (c) survival and (d) increases in number of leaves of *Maianthemum* plants (means and standard error bars). Sites arranged from low to high elevation; different uppercase letters indicate significant overall differences between sites and different lower-case letters indicate differences between environments within a site ($p < 0.05$).

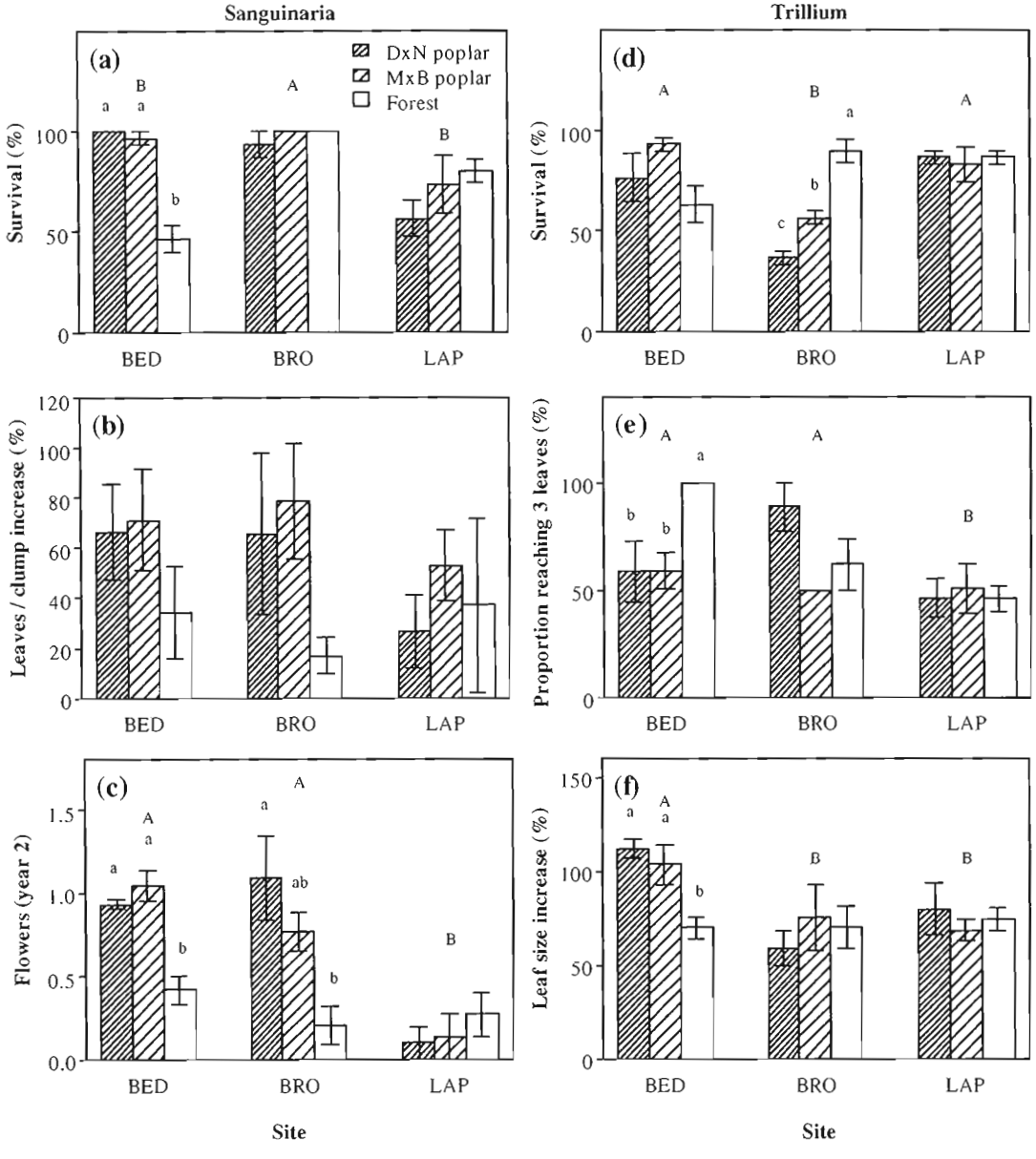

Figure 3.3 Responses of *Sanguinaria canadensis* and *Trillium grandiflorum* one year after transplantation into plantations of two hybrid poplar clones and natural woodlots at three sites. (a) Survival, (b) relative increase in number of leaves, and (c) number of flowers in year 2 of *Sanguinaria* clumps; (d) survival, (e) proportion of one-leaf plants passing into the three-leaf stage, and (f) relative increase in leaf size of *Trillium* plants; means and 95% confidence intervals; DxN poplar: plantation of a DxN poplar clone; MxB poplar: plantation of an MxB poplar clone; forest: second-growth hardwood woodlot. Different uppercase letters indicate significant overall differences between sites and different lower-case letters indicate differences between environments within a site ($p < 0.05$).

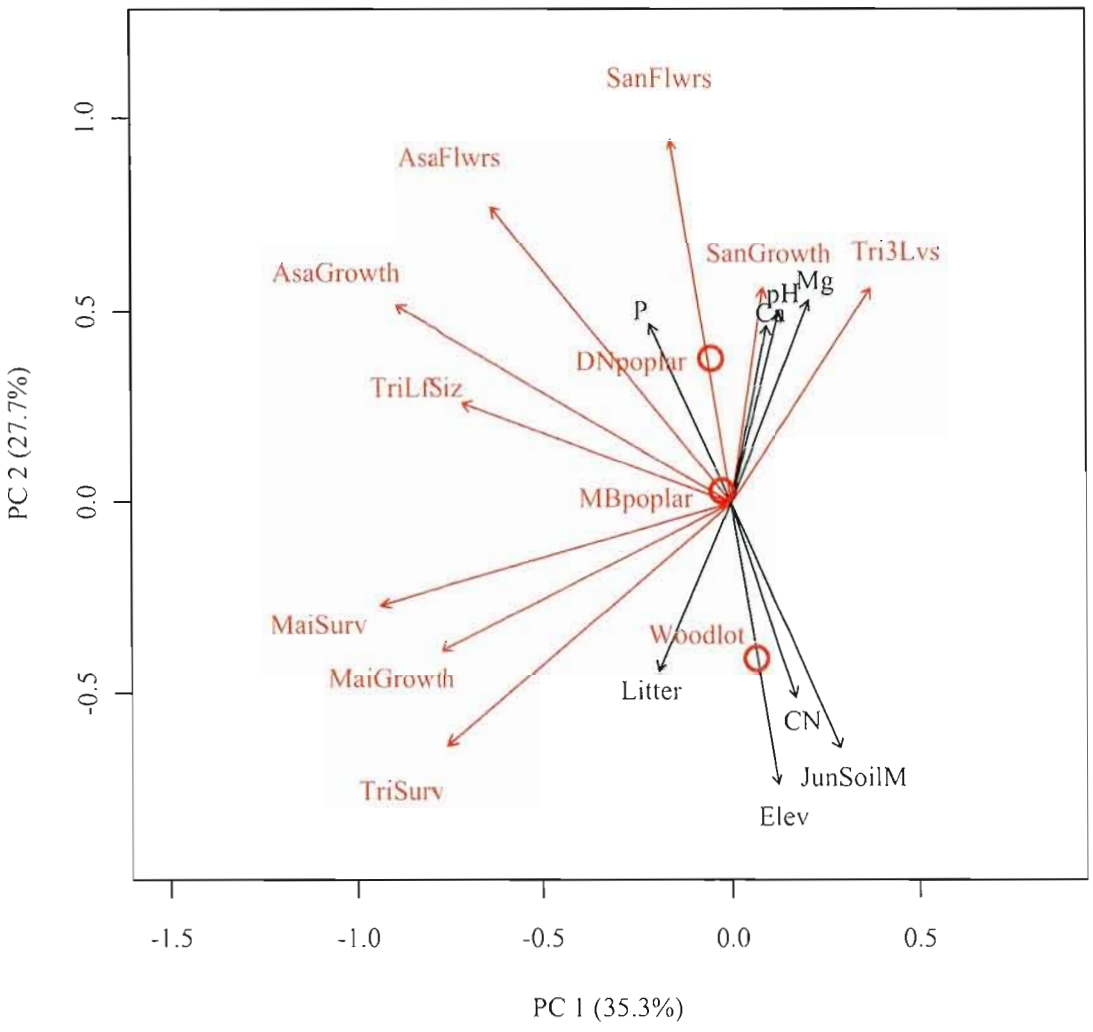

Figure 3.4 The first two principal components of survival, relative growth, and flowering of four planted herbaceous species in plantations of two hybrid poplar clones and natural woodlots at three transplantation sites (Bedford, Bromptonville, and La Patrie). Species response variables are represented by red arrows and significant fitted environmental characteristics ($p<0.05$) by black arrows. Asa: *Asarum canadense*; Mai: *Maianthemum racemosum*; San: *Sanguinaria canadensis*; Tri: *Trillium grandiflorum*; Surv: survival rate; Growth: relative increase in number of leaves per plot (*Asarum*) or per plant (all other species); LfSize: relative increase in average leaf size; AsaFlwrs: relative increase in number of flowers per plot; SanFlwrs: number of flowers in year 2; Tri3Lvs: proportion of one-leaved Trillium plants transitioning to the three-leaf stage in the second year after planting; DNpoplar, MBpoplar: 10 year old hybrid poplar plantations of a DxN clone and MxB clone respectively; Forest: second-growth hardwood woodlot; Elev: site elevation; Litter: leaf litter biomass in late fall; JunSoilM: soil moisture content by weight at 10cm depth in June; P, Mg, Ca: log-transformed soil nutrient concentrations, CN: soil carbon:nitrogen ratio, pH: soil pH.

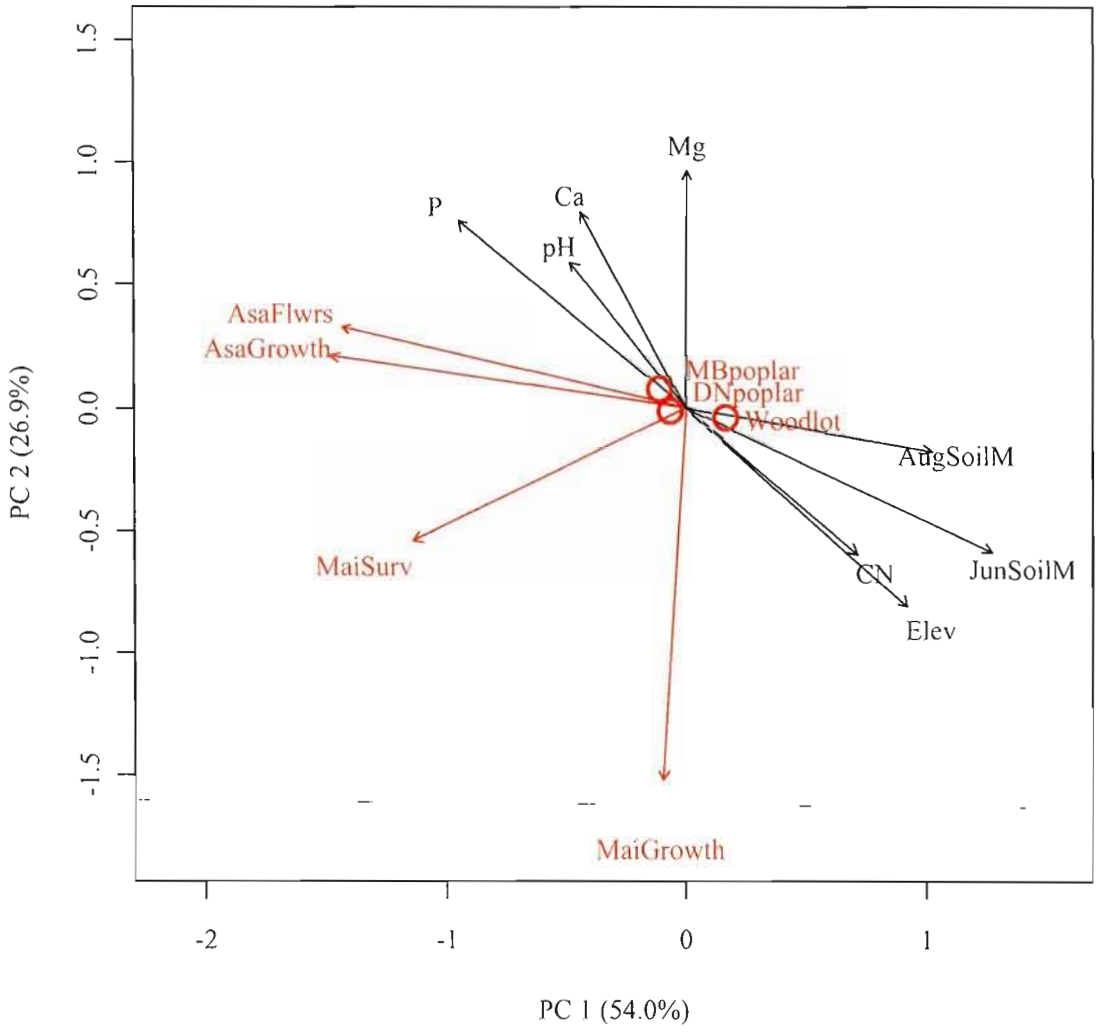

Figure 3.5 The first two principal components of survival and relative growth measures after one year of *Asarum canadense* and *Maianthemum racemosum* in plantations of two hybrid poplar clones and natural woodlots at six sites. Species response variables are represented by red arrows and significant fitted environmental characteristics ($p<0.05$) by black arrows. MaiSurv: *Maianthemum* survival rate; MaiGrowth: relative increase in number of *Maianthemum* leaves per plant; AsaGrowth, AsaFlwrs: relative increase in number of *Asarum* leaves and flowers respectively per plot; DNpoplar, MBpoplar: 10 year old hybrid poplar plantations of a DxN clone and MxB clone respectively; Forest: second-growth hardwood woodlot; Elev: site elevation; JunSoilM, AugSoilM: soil moisture content by weight at 10cm depth in June and August; P, Mg, Ca: log-transformed soil nutrient concentrations, CN: soil carbon:nitrogen ratio.

CHAPTER IV

GENERAL CONCLUSION

The two studies presented in this thesis investigated the changes produced in the understory of hybrid poplar plantations compared to natural reforestation of abandoned fields. The results elucidate a number of possible ecological effects of hybrid poplar plantations when planted on abandoned fields.

All of the hybrid poplar plantations in this study succeeded in accelerating the development of a tree canopy, along with increased shading and leaf litter production, compared to unplanted abandoned fields. However, the acceleration was much greater in the more productive plantations, under which the levels of shading and leaf litter attained those of the natural woodlots. With less light and more leaf litter, the total cover of the herb and shrub layer vegetation in these plantations was reduced (especially under the MxB hybrid poplars), which potentially created better opportunities for colonization by shade-tolerant species. Accordingly, the more productive plantations showed a shift in species composition compared to the abandoned fields and the less productive plantations, with a slight increase in the relative abundance of species found in the woodlots, and a slight decrease in the abundance of abandoned field species. Furthermore, the plantations appeared to accelerate the creation of favourable conditions for colonization by tree species. Despite the fact that large differences remained between the species composition in the plantations and the woodlots, these differences may not solely reflect a difference in the environment; rather, dispersal limitations may have prevented the colonization of the plantations thus far by many forest understory species, limiting the rate at which understory communities can develop as a response to changing environmental conditions under the plantation canopies. The results of

the transplant experiment gave support to this hypothesis, showing that certain forest understory species can survive, grow, and flower equally well in the plantations as in the natural woodlots, at least during the adult life stages.

However, it is equally possible that differences in the understory environment between the plantations and the woodlots had contributed to the lack of successful colonization of the plantations by many forest understory species, particularly at the seedling emergence and establishment stage, which was not evaluated in these studies. First, the changes in soil chemical properties that are normally associated with reforestation appear to be slow to occur, despite the rapid growth of trees. Thus, the soils under the hybrid poplar plantations in this study remained very different from the soils under forest stands of natural origin. Second, the rapidly growing hybrid poplar trees may have a higher rate of transpiration than either the trees of natural forest stands or the herbaceous and shrub vegetation of abandoned fields. This increase in transpiration may have resulted in less soil moisture being available for understory plants during summer droughts. However, it was not possible in this study to separate the effects of evapotranspiration from drainage, and the lower soil moisture in the plantations compared to the woodlots may have been simply due to a better drainage of these soils. Third, the litter quality of the hybrid poplars (especially of the MxB clone), though not measured in this study, may have been different from the litter of the mixed hardwood forest, resulting in differences in nutrient availability, soil microbial and faunal communities, and/or concentrations of various chemical compounds in the soil. All of these differences in abiotic factors could affect the quality of the understory habitat for native plant species. Moreover, changing environmental conditions and biotic interactions in future years of the transplant experiment could expose as yet unobserved critical differences between the habitats, or conversely reveal a convergence of the attributes of the two habitats.

The results of this thesis also highlight the importance of site selection for plantations: the plantations on poorer, longer-abandoned sites tended to provide less of an advantage than the plantations on richer, recently-abandoned sites in terms of accelerating the creation of a forest understory environment. Since vegetation communities on long-abandoned sites have already progressed through several stages of succession, the disturbances associated with the preparation of these sites can have an important retrogression effect on succession, favouring

the return of early successional species, while the slow growth of the plantation trees on these sites limits their potential accelerating effect. Thus, on the poorer sites in this study, the plantations continued to resemble the abandoned fields in terms of vegetation composition and total cover of the herb and shrub layer, although the poplars did increase shading and leaf litter biomass compared to the unplanted fields, implying that a change in the vegetation may be observed in later years as these plantations continue to develop.

The choice of clone may also be important for attaining restoration or NTFP production objectives within a hybrid poplar plantation. Little difference was observed in these studies between the MxB and the DxN clones; however, the MxB clone did produce slightly more shade and leaf litter, and in the more productive plantations was characterized by a much lower total cover of the herb and shrub layer vegetation. On the other hand, the MxB clone supported more introduced species, and it has been hypothesized that secondary chemicals in its leaf litter may inhibit the growth of other plant species. Although no difference was observed between the clones in the transplant experiment, the re-expansion of the root systems after the initial site preparation may produce different effects in later years. More research is needed to test these hypotheses and fully evaluate the suitability of MxB hybrid poplar clones for understory vegetation.

On a more general level, more research is needed to better understand the effects of hybrid poplar plantations on the understory environment and their value as habitat for understory plant species. However, one conclusion that can be drawn from these results is that hybrid poplar plantations on abandoned farmland have the potential to facilitate tree species colonization. This potential can be utilized to accelerate the transition to a natural forest stand if naturally colonizing tree seedlings and saplings are allowed to mature and form the next generation of canopy trees after the harvest of the hybrid poplar trees. Another promising result of this research is the potential for cultivating native forest herbs as non-timber forest products in hybrid poplar plantations. NTFP production does not require that a species complete its life cycle, but only that the plants can grow from seedlings to maturity, while seeds may be germinated off-site. The use of hybrid poplar plantations could be a less costly alternative to artificial shade structures, while at the same time increasing the revenue potential of a plantation.

It is likely that many abandoned fields in southern Quebec (and also in south-eastern Ontario and adjacent New England states) resemble the fields used in these studies, and that landowners wishing to restore certain forest attributes could replicate these results using hybrid poplar plantations on their properties. For a landowner interested in practising forestry, cultivating non-timber forest products, or restoring a high-value forest ecosystem, the afforestation of an abandoned field may potentially be a more interesting option than using existing woodlots, which on many properties are on poorly drained land or otherwise of little value. This option becomes especially useful at lower elevations, where land-use pressure from agriculture is stronger and existing woodlots are rarer and more likely to be of poor quality. Despite the many questions that remain to be answered, the results of this thesis suggest that on recently-abandoned, productive sites, hybrid poplar plantations appear to be a promising avenue for active afforestation.

APPENDIX A

CANOPY SPECIES COMPOSITION OF WOODLOT PLOTS

Table A.1 Tree species composition of woodlot plots at eight study sites in the Eastern Townships region of Quebec, Canada. At each site, percent basal area (frequency (%)) of important tree species (having a frequency > 33% at one or more sites) and total tree basal area are shown. For each site, dominant species (> 25% of total basal area) are in bold.

	Site															
Species	Bedford		Bromptonville		Ste-Catherine		Ogden		St-Adrien		Melbourne		La Patrie		Stornoway	
Abies balsamea			5.1	(66)			5.4	(100)							1.6	(66)
Acer rubrum	**51.2**	(66)	5.7	(66)	**26.6**	(100)	**37.7**	(100)	4.5	(33)	3.9	(66)	7.6	(33)		
Acer saccharum					10.1	(33)			**36.2**	(100)	3.1	(66)	**85.1**	(100)		
Betula alleghaniensis					2.1	(33)	3.1	(66)	**45.2**	(100)	16.3	(66)	7.3	(66)		
Betula papyrifera							**26.6**	(100)								
Betula populifolia			3.0	(33)	4.6	(66)					2.5	(33)			10.4	(33)
Fagus grandifolia					0.2	(33)										
Fraxinus americana	**25.4**	(66)	**74.8**	(100)	13.6	(66)	6.7	(33)	12.3	(66)	**38.5**	(100)				
Malus sp.					1.1	(66)					6.7	(66)			7.7	(66)
Picea glauca															**42.4**	(100)
Populus tremuloides	6.0	(33)			0.8	(66)									16.3	(66)
Prunus serotina			7.4	(100)	0.2	(33)					4.7	(100)			21.6	(33)
Quercus rubra					**39.6**	(100)										
Sorbus americana					0.2	(33)					22.5	(100)				
Thuja occidentalis	3.9	(33)					16.5	(66)								
Ulmus americana	8.6	(33)	2.1	(66)	1.0	(66)	3.5	(33)			1.2	(33)				
Total tree basal area (m^2/ha)	22.3		18.1		51.3		22.2		27.8		29.4		32.4		17.0	

REFERENCES FOR GENERAL INTRODUCTION AND CONCLUSION

Aubin, I., C. Messier and A. Bouchard. 2008. Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biological Conservation **141**(10): 2461-2476.

Batish, D.R., H.P. Singh and R.K. Kohli. 2001. Vegetation exclusion under *Casuarina equisetifolia* L.: Does allelopathy play a role? Community Ecology **2**(1): 93-100.

Bélanger, L. and M. Grenier. 2002. Agriculture intensification and forest fragmentation in the St. Lawrence valley, Québec, Canada. Landscape Ecology **17**(6): 495-507.

Benjamin, K., A. Bouchard and G. Domon. 2007. Abandoned farmlands as components of rural landscapes: An analysis of perceptions and representations. Landscape and Urban Planning **83**(4): 228-244.

Benjamin, K., A. Bouchard and G. Domon. 2008. Managing abandoned farmland: The need to link biological and sociological aspects. Environmental Management **42**(4): 603-619.

Benjamin, K., G. Domon and A. Bouchard. 2005. Vegetation composition and succession of abandoned farmland: Effects of ecological, historical and spatial factors. Landscape Ecology **20**: 627-647.

Bobiec, A. 1998. The mosaic diversity of field layer vegetation in the natural and exploited forests of Bialowieza. Plant Ecology **136**(2): 175-187.

Brockerhoff, E.G., H. Jactel, J.A. Parrotta, C.P. Quine and J. Sayer. 2008. Plantation forests and biodiversity: Oxymoron or opportunity? Biodiversity and Conservation **17**(5): 925-951.

Brunet, J. and G. Von Oheimb. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology **86**(3): 429-438.

CAAAQ. 2008. Agriculture et agroalimentaire : assurer et bâtir l'avenir, Commission sur l'avenir de l'agriculture et de l'agroalimentaire québécois: 274.

Charron, D. and D. Gagnon. 1991. The Demography of northern populations of *Panax quinquefolium* (American ginseng). Journal of Ecology **79**(2): 431-445.

Chazdon, R.L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science **320**(5882): 1458-1460.

Cole, R.J., K.D. Holl and R.A. Zahawi. 2010. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecological Applications **20**(5): 1255-1269.

Coulombe, G., J. Huot, J. Arseneault, E. Bauce, J.-T. Bernard, A. Bouchard, M.A. Liboiron and G. Szaraz. 2004. Commission d'étude sur la gestion de la forêt publique québécoise, Bibliothèque nationale du Québec.

Côté, P., R. Tittler, C. Messier, D.D. Kneeshaw, A. Fall and M.J. Fortin. 2010. Comparing different forest zoning options for landscape-scale management of the boreal forest: Possible benefits of the TRIAD. Forest Ecology and Management **259**(3): 418-427.

D'Orangeville, L., A. Bouchard and A. Cogliastro. 2008. Post-agricultural forests: Landscape patterns add to stand-scale factors in causing insufficient hardwood regeneration. Forest Ecology and Management **255**(5-6): 1637-1646.

De Keersmaeker, L., L. Martens, K. Verheyen, M. Hermy, A. De Schrijver and N. Lust. 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). Forest Ecology and Management **188**(1-3): 291-304.

Dölle, M. and W. Schmidt. 2009. Impact of tree species on nutrient and light availability: Evidence from a permanent plot study of old-field succession. Plant Ecology **203**(2): 273-287.

Domon, G. and A. Bouchard. 2007. The landscape history of Godmanchester (Quebec, Canada): Two centuries of shifting relationships between anthropic and biophysical factors. Landscape Ecology **22**(8): 1201-1214.

Dzwonko, Z. 2001. Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. Ecography **24**(2): 198-204.

Dzwonko, Z. and S. Loster. 1992. Species richness and seed dispersal to secondary woods in southern Poland. Journal of Biogeography **19**(2): 195-204.

Fahy, O. and M. Gormally. 1998. A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. Forest Ecology and Management **110**(1-3): 263-273.

Ferris, R., A.J. Peace,J.W. Humphrey and A.C. Broome. 2000. Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. Forest Ecology and Management **136**(1-3): 35-51.

Flinn, K.M. and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment **3**(5): 243-250.

Gachet, S., A. Leduc, Y. Bergeron, T. Nguyen-Xuan and F. Tremblay. 2007. Understory vegetation of boreal tree plantations: Differences in relation to previous land use and natural forests. Forest Ecology and Management **242**(1): 49-57.

Gleeson, S.K. and D. Tilman. 1990. Allocation and the transient dynamics of succession on poor soils. Ecology **71**(3): 1144-1155.

Honnay, O., K. Verheyen,J . Butaye, H. Jacquemyn, B. Bossuyt and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters **5**(4): 525-530.

Hooker, T.D. and J.E. Compton. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecological Applications **13**(2): 299-313.

Jeffries, S.B., T.R. Wentworth and H.L. Allen. 2010. Long-term effects of establishment practices on plant communities across successive rotations in a loblolly pine (*Pinus taeda*) plantation. Forest Ecology and Management **260**(9): 1548-1556.

Jobbágy, E.G. and R.B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications **10**(2): 423-436.

Laganière, J., D.A. Angers and D. Paré. 2010. Carbon accumulation in agricultural soils after afforestation: A meta-analysis. Global Change Biology **16**(1): 439-453.

Le Houérou, H.N. 1993. Land degradation in Mediterranean Europe: can agroforestry be a part of the solution? A prospective review. Agroforestry Systems **21**(1): 43-61.

Mansourian, S., D. Lamb and D. Gilmour. 2005. Overview of technical approaches to restoring tree cover at the site level. In Mansourian, S., D. Vallauri and N. Dudley, eds. Forest restoration in landscapes: Beyond planting trees.. New York, Springer: 241-249.

Marchand, P.P. and S. Masse. 2007. Boisement et agroforesterie en courtes rotations en territoire privé au Québec : Examen des lois, règlements, politiques et programmes, Ressources naturelles Canada, Service canadien des forêts, Centre de foresterie des Laurentides.

Matlack, G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology **75**(5): 1491-1502.

Ministère du Développement durable, de l'Environnement et des Parcs du Québec. 2010. Plantes menacées ou vulnérables au Québec. Retrieved December 11, 2010, from http://www.mddep.gouv.qc.ca/biodiversite/especes/.

Nantel, P., D. Gagnon and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments Conservation Biology **10**(2): 608-621.

Nault, A. and D. Gagnon. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. Journal of Ecology **81**(1): 101-119.

Paquette, A. and C. Messier. 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment **8**(1): 27-34.

Paquette, A., C. Messier, P. Périnet and A. Cogliastro. 2008. Simulating light availability under different hybrid poplar clones in a mixed intensive plantation system. Forest Science **54**: 481-489.

Parrotta, J.A., J.W. Turnbull and N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management **99**(1-2): 1-7.

Peterken, G.F. 2000. Rebuilding networks of forest habitats in lowland England. Landscape Research **25**(3): 291-303.

Pickett, S.T.A. 1982. Population patterns through twenty years of oldfield succession. Plant Ecology **49**(1): 45-59.

Poulton, P.R., E. Pye, P.R. Hargreaves and D.S. Jenkinson. 2003. Accumulation of carbon and nitrogen by old arable land reverting to woodland. Global Change Biology **9**(6): 942-955.

Poyatos, R., J. Latron and P. Llorens. 2003. Land use and land cover change after agricultural abandonment: The case of a Mediterranean Mountain area (Catalan Pre-Pyrenees). Mountain Research and Development **23**(4): 362-368.

Richter, D.D., D. Markewitz, C.G. Wells, H.L. Allen, R. April, P.R. Heine and B. Urrego. 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. Ecology **75**(5): 1463-1473.

Robertson, G.P. and P.M. Vitousek. 1981. Nitrification potentials in primary and secondary succession. Ecology **62**(2): 376-386.

Roura-Pascual, N., P. Pons,M. Etienne and B. Lambert. 2005. Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. Mountain Research and Development **25**(3): 252-261.

Singleton, R., S. Gardescu,P.L. Marks and M.A. Geber. 2001. Forest herb colonization of postagricultural forests in central New York State, USA. Journal of Ecology **89**(3): 325-338.

Soo, T., A. Tullus, H. Tullus and E. Roosaluste. 2009. Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments. Forest Ecology and Management **257**(3): 858-867.

Soucy-Gonthier, N., D. Marceau, M. Delage, A. Cogliastro, G. Domon and A. Bouchard. 2003. Détection de l'évolution des superficies forestières en Montérégie entre juin 1999 et août 2002 à partir d'images satellitaires Landsat-TM - rapport présenté à l'Agence forestière de la Montérégie (AFM), directeur : Luc Dumouchel.

Souto, X.C., J.C. Bolaño, L. González and M.J. Reigosa. 2001. Allelopathic effects of tree species on some soil microbial populations and herbaceous plants. Biologia Plantarum **44**(2): 269-275.

Stephens, S.S. and M.R. Wagner. 2007. Forest plantations and biodiversity: A fresh perspective. Journal of Forestry **105**(6): 307-313.

Stevens, A. and B. van Wesemael. 2008. Soil organic carbon stock in the Belgian Ardennes as affected by afforestation and deforestation from 1868 to 2005. Forest Ecology and Management **256**(8): 1527-1539.

Summers, R.W., R.A. Mavor, A.M. MacLennan and G.W. Rebecca. 1999. The structure of ancient native pinewoods and other woodlands in the Highlands of Scotland. Forest Ecology and Management **119**(1-3): 231-245.

Thorne, J.F. and S.P. Hamburg. 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. Ecology **66**(4): 1333-1338.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**(3): 190-214.

Truax, B., F. Lambert and D. Gagnon. 2000. Herbicide-free plantations of oaks and ashes along a gradient of open to forested mesic environments. Forest Ecology and Management. **137**: 155-169.

Verheyen, K. and M. Hermy. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. Journal of Vegetation Science **15**(1): 125-134.

Vouligny, C. and S. Gariépy. 2008. Les friches agricoles au Québec: état des lieux et approches de valorisation. Ottawa, Agriculture and Agri-food Canada